PROTEIN STATUS OF MUSKOXEN AND CARIBOU

IN LATE WINTER

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ABSTRACT

The conservation and management of northern ungulates depends upon our understanding of the influence of habitat associations on the nutritional condition of individuals and population productivity. Adverse foraging conditions in late winter may reduce the availability of body proteins for reproduction. Therefore, assessing nitrogen (N) or protein status in late winter could be a valuable tool to monitor populations of northern ungulates. I collected >1,800 excreta samples to evaluate isotopic metrics of protein status [proportion of serum amino acid N derived from body N (*p*-AN), proportion of urea N derived from body N (*p*-UN), and the difference between the isotopic ratios of N ($\delta^{15}N$) in body tissues and urinary urea ($\Delta_{Body\text{-}urea}$)] in captive and wild populations of muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) in late winter. I evaluated the dynamics of body protein and $\delta^{15}N$ in a captive population of female muskoxen (2007). Diets and protein status were assessed in populations of wild muskoxen in northern Alaska (2005-2008); a semi-captive (penned) population of wild, pregnant caribou (2006); and wild populations of migratory and sedentary ecotypes of caribou (2006-2008). Captive female muskoxen lost body protein (~6%) in late gestation and these losses corresponded with the protein deposited in reproductive tissues. The concentration of plasma urea, the *p*-AN, and *p*-UN tended to increase throughout winter. During late gestation, most penned pregnant caribou on an *ad libitum* feeding schedule lost core body mass (55%) and were in negative protein status (54%). For groups of wild muskoxen ($n = 30$), abundance of preferred forages improved protein status (*p*-UN; $R^2 = 0.45$). At the foraging sites of wild caribou ($n = 32$), the amount of shrubs in a lichen-rich diet had a positive effect on protein status ($\Delta_{Body\text{-}urea}$, $r^2 = 0.26$). Foraging constraints in late winter will decrease the amount of body proteins available for reproduction. However, considerable challenges remain to applying the *p*-UN as a monitoring tool at broad scales for caribou, but with appropriate consideration, isotopic proxies may be used to evaluate environmental constraints for northern ungulates at small scales.

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CHAPTER 1 - INTRODUCTION

Introduction

The conservation and management of wildlife depends upon our understanding of the link between the physiology of individuals and the dynamics of their population (Gaston et al. 2009). The effects of intra-specific competition and subsequent changes in resource availability and nutritional limitation on reproduction and survival form the theoretical underpinnings of contemporary models of population growth (e.g., Caughley 1970, Clutton-Brock 1982, McCullough 2002). However, nutritional contributions to population changes are often obscured by delays in the response of a population (Post et al. 2002), interactions between density-dependent and -independent factors (Jacobsen et al. 2004), spatial variance in resource distribution and quality (Wang et al. 2006), and predation (Wang et al. 2009).

Despite these challenges, it is imperative that we increase our understanding of the nutritional contributions to population changes of ungulates, particularly at high latitudes where the rate of environmental change and the impacts of a changing climate are most pronounced (National Research Council 2008). Northern ungulates are an important subsistence resource for rural and aboriginal peoples throughout the circumpolar north (Klein et al. 2005, Hummel and Ray 2008). Consequently, resource management agencies and communities in North America and Eurasia are tasked with monitoring the status and trends of populations of northern herbivores. Challenges include establishing baseline conditions and identifying population parameters that are cost effective and reliable indicators of population trajectories at small temporal scales (Klein et al. 2005, Post and Forchhammer 2006).

Nutritional condition is an important determinant of productivity in northern ungulates (Cameron and Ver Hoef 1994, Adamczewski et al. 1998, McArt et al. 2009). High seasonal variation in plant abundance accentuates the need for northern ungulates to replenish body stores during a short growing season that is critical for winter survival (Adamczewski et al. 1997, Chan-McLeod et al. 1999, Barboza and Hume 2006). Body

fat is the primary energy store of ungulates (Price and White 1985). Body proteins are primarily used as a source of N for maintenance of critical tissues and reproduction (Chan-McLeod et al. 1995, Gerhart et al. 1996, Barboza and Parker 2008) but may be used for energy if fat stores are depleted (Barboza et al. 2009). Body stores of non-reproductive animals approach their annual minima in late winter (Chan-McLeod et al. 1999, Barboza et al. 2004), whereas stores of reproductive females continue to decline due to the additional nutritional costs of gestation (Oftedal 1985).

Nutritional restrictions during the last trimester of pregnancy (late winter) can impair fetal growth and development (Rognmo et al. 1983, Sams et al. 1995). Thus, females may produce small offspring (Reimers 1997, Festa-Bianchet et al. 1998, Adams 2005) with poor survivorship (Albon et al. 1987, Skogland 1990). Growth of offspring can be impaired by nutritional restriction of the mother during pregnancy and early lactation (Albon et al. 1987, Mech et al. 1987, Forchhammer et al. 2002, Adams 2003). Demands for energy and N increase progressively through late winter for reproductive females as most fetal tissues are deposited in the last trimester and milk production increases after parturition (Oftedal 1985). Annual N demands peak during lactation for adult females but these demands generally cannot be met by intake alone and require the use of body stores (Chan-McLeod et al. 1994, White et al. 1997, Barboza and Parker 2008). Indeed, neonatal growth rates are directly correlated with the protein content of maternal milk (Robbins et al. 1981). During periods of prolonged or excessive restrictions in forage in late winter, females may allocate protein to maintain their own body tissues rather than depositing protein in offspring (Festa-Bianchet and Jorgenson 1998, Chan-McLeod et al. 1999, Adams 2005). Therefore, the ability of reproductive females to maintain maternal stores of N in body protein is crucial for the production, growth, and survival of offspring (Allaye-Chan 1991, Landete-Castillejos et al. 2001, Barboza and Parker 2008). Consequently, estimates of N status or balance (protein status or balance) in late winter may offer a valuable tool to assess productivity.

Seasonal changes in body protein, however, are difficult to measure and detect because the changes are small relative to the total mass of body protein (Torbit et al.

1985, Chan-McLeod et al. 1994, Gerhart et al. 1996). Additionally, most techniques to assess protein status are impractical for large animals in the wild because they require cross-sectional comparisons of body composition among large numbers of animals (e.g., seasonal harvests; Chan-McLeod et al. 1994, Gerhart et al. 1996) or repeated measures of body composition in the same animal (e.g., estimates of body water content, Parker et al. 1993b; ultrasound measurements of loin thickness, Cook et al. 2001). Although clearly valuable, these techniques may be precluded by the logistical and financial challenges of working in remote areas as well as biological (e.g., small populations), legal (e.g., conservation mandates), ethical (e.g., animal safety or humaneness) or cultural (e.g., subsistence use) constraints.

Excreta in snow-based techniques currently offer the best potential to non-invasively assess the protein status of northern ungulates in remote areas during winter. The ratios of urinary metabolites (e.g., allantoin, cortisol, glucuronic acid, potassium, and urea) in snow relative to creatinine have been used with mixed success (see review in Parker 2003) to evaluate various metrics of condition in ungulates (e.g., DelGiudice et al. 1989, Saltz and White 1991, Parker et al. 1993a, DelGiudice et al. 2000, Servello and Schneider 2000, Larter and Nagy 2001, Säkkinen et al. 2001). For northern ungulates, however, some ratio-based approaches may be confounded by changes in renal function that affect excretion rates of urinary urea and creatinine (e.g., Säkkinen et al. 2001).

Nitrogen isotopes in excreta have been used to discriminate between sources of N in urinary urea to assess protein status in captive reindeer (*Rangifer tarandus*, Barboza and Parker 2006). Urinary urea is derived from two sources of N: diet and body proteins. Dietary proteins are typically depleted in ^{15}N compared to body proteins (Kelly 2000, Caut et al. 2009). A linear-mixing model (Karasov and Martinez del Rio 2007) can be used to estimate the relative contributions of N from the diet (depleted ^{15}N) and the body (enriched ^{15}N) to urea (Barboza and Parker 2006). Fractions of plant fibers in fecal samples can be used to estimate $\delta^{15}N$ of the diet. Urinary creatinine is a muscle metabolite that is used to estimate the $\delta^{15}N$ of red blood cells (body proteins). As animals rely more heavily on body proteins to meet metabolic demands, the $\delta^{15}N$ of urea

increases, and consequently, the proportion of urinary urea N that is derived from body N increases (*p*-UN, Barboza and Parker 2006). Thus, this isotopic technique can provide estimates of $\delta^{15}N$ of urinary metabolites, dietary and body N, and the protein status (*p*-UN) of individual animals. However, this isotopic approach has not been applied to wild populations of northern ungulates [e.g. muskoxen (*Ovibos moschatus*) and caribou (*R. tarandus*)].

Muskoxen and Caribou

Muskoxen and caribou exhibit divergent adaptations to surviving and reproducing in the austere and uncertain conditions of arctic and sub-arctic winters. Muskoxen typically inhabit coastally-influenced environments in moist graminoid- and willow (*Salix* spp.)- dominated vegetative associations (Gunn and Adamczewski 2003). Muskoxen are sedentary (Jingfors 1982, Nellemann 1998), large-bodied grazers (Hofmann 2000) that establish, conserve, and use large body stores to survive and reproduce (Klein 1992, Adamczewski et al. 1997, Lawler and White 1997, White et al. 1997, Gunn and Adamczewski 2003). Timing of parturition is usually asynchronous in wild populations (Tener 1965, Rowell et al. 1993, Reynolds 2001). Female muskoxen typically give birth and lactate 0-8 weeks prior to the availability of plant re-growth (Gray 1987). Consequently, females rely exclusively on body stores to produce a fetus and nurse a calf (White et al. 1989, White et al. 1997).

Unlike muskoxen, caribou display a marked diversity in adaptations to surviving and reproducing in northern environments. Caribou are a medium-sized herbivore that dwell in forests and tundra from coasts to mountain ranges over a large latitudinal gradient (50 to 80° N; Blix 2005). Diverse behavioral (degrees of migration and gregariousness, Bergerud 1996) and physiological adaptations (e.g., reproductive timing and investments, Barboza and Parker 2008) are used to respond to changes in environmental conditions, forage availability, and the risk of predation. Similar to muskoxen, female caribou produce a fetus almost exclusively from body stores, but the timing of birth may be more synchronous and coincides closely with the spring re-growth

of plants (Barboza and Parker 2008). Therefore, females are able to offset the substantial nutritional demands of lactation with the availability of highly digestible and nutritious forages (White and Luick 1984). Although the adaptations of muskoxen and caribou to northern environments differ, the availability of body protein for reproduction may constitute a nutritional "bottleneck" for both species (White et al. 1989, White et al. 1997, Barboza and Parker 2008).

Goal, Objectives, Hypotheses, and Predictions

My goals were 1) to evaluate and refine the use of a non-invasive, isotopic approach to assess the protein status of wild populations of muskoxen and caribou and 2) identify characteristics of diet and physiography for wild muskoxen and caribou that have the potential to affect population productivity. The subsequent chapters (2-5) address these goals in the format of separate manuscripts for publication in peer-reviewed journals. These chapters are the result of collaboration with biologists from Alaska and Canada. To recognize those contributions, **CHAPTERS 2** through **5** are co-authored for publication. My co-authors participated in securing funding and resources for laboratory analyses and sample collection, and in editing and reviewing drafts of each manuscript. As lead author, I served the principal role in implementation, analysis, interpretation and preparation of each manuscript.

In **CHAPTER 2**, I conducted an experiment on captive female muskoxen at the Large Animal Research Station in Fairbanks, Alaska. My objective was to evaluate the protein dynamics of captive female muskoxen by measuring body composition over late gestation, the birth masses of their calves, and N isotopes in serum amino acids and urinary urea. I hypothesized that as capital breeders, female muskoxen rely exclusively on endogenous sources of protein for late gestation and early parturition. Therefore I predicted that pregnant females would lose body protein in late winter, whereas non-pregnant controls would maintain or regain stores of body protein. I hypothesized that maternal loss of protein was associated with the development of fetal and uterine tissues. Consequently, I predicted that losses of body protein in pregnant animals would be

similar to the protein deposited in reproductive tissues. I hypothesized that pools of N in amino acids and urea in pregnant animals would reflect body protein rather than dietary protein. Therefore, I predicted that proportions of amino-N and urea-N that were derived from body protein would be greater in pregnant than non-pregnant females.

In **CHAPTER 3**, I present the first application of this isotopic technique to wild muskoxen. I estimated the protein status of groups of muskoxen in 3 populations (North Slope, Cape Thompson, and Seward Peninsula) in northern Alaska from 2005 to 2008. My objective was to evaluate aspects of winter habitat that may affect protein status in wild muskoxen. I used published studies to construct an ecologically plausible set of models to explain the observed variance in protein status among groups of muskoxen. An information-theoretic approach was used to evaluate these competing models. I predicted that models with population or year would reflect a response to demographic or environmental constraints, whereas models associated with forage availability at smaller scales would be more apparent if proxies of localized foraging conditions were better correlates of protein status.

My objectives in **CHAPTER 4** were to assess the isotopic proxies of diet and protein status in a semi-captive population of pregnant caribou in the Chisana Herd (Alaska and Yukon Territory) and to identify the potential challenges of population-level assessments of protein status in wild caribou. I hypothesized that the composition of the diet could be indexed by the $\delta^{15}N$ of the feces. Thus, I predicted that the $\delta^{15}N$ of plant residues in the feces would correspond to the proportion of major forages in the diet. I hypothesized that foraging conditions in winter would affect protein status in pregnant caribou. Therefore, I predicted that pregnant caribou in the exclosure would generally be in positive protein status as a result of supplemental feeding.

In **CHAPTER 5**, I present the first application of isotopic approaches to monitor wild populations of migratory and sedentary caribou in 4 herds (Central Arctic, Western Arctic, Chisana, and Denali) from 2006 to 2008. My objectives were to establish a baseline for monitoring efforts and to identify and discuss any potential nutritional correlates of wintering habitats in caribou. I compared the characteristics of the diet and

terrain, isotopic parameters, and proxies of protein status by ecotype, herd, year, and foraging site. Published studies were used to construct an ecologically plausible set of models to explain the observed variance in protein status among groups of caribou and an information-theoretic approach was used to evaluate support for competing models.

In **CHAPTER 6**, I present my general conclusions on the use of isotopes of N to assess the protein status in wild populations of muskoxen and caribou, the nutritional correlates of winter habitats in these ungulates, as well as the potential applications and constraints of isotopic techniques to monitor populations of northern ungulates.

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CHAPTER 2 - DYNAMICS OF BODY PROTEIN AND THE IMPLICATIONS FOR REPRODUCTION IN CAPTIVE MUSKOXEN (*OVIBOS MOSCHATUS*) DURING WINTER[a]

Abstract

Muskoxen are considered obligate capital breeders, in that they rely exclusively on endogenous stores to reproduce. We studied 14 captive female muskoxen ($n = 9$, not pregnant; $n = 5$, pregnant) in February-June 2007 to assess changes in body composition and isotopic correlates of protein status [proportions of amino acid (*p*-AN) and urea N (*p*-UN) derived from body N]. We measured body mass, body composition, and N metabolites in blood and urine between mid-gestation in February and early lactation (Postcalving). All muskoxen lost body mass (-6 to -12%) and fat (-22 to -24%) over the winter while pregnant muskoxen lost body protein (-6%) in late gestation; non-pregnant animals maintained stores of body protein (+6%) in late winter. Losses of body protein in pregnant muskoxen (255 ± 71.5 mg protein·kg $^{-0.75}$·d^{-1}) were similar to the amount of protein deposited in reproductive tissues (319 ± 33.4). Plasma urea concentration increased (27 to 59 mg·dL^{-1}) with *p*-UN (0.13 to 0.33), which indicated oxidation of amino N during late winter. High estimates of *p*-AN (0.72 ± 0.07) indicated that amino N from body protein was reutilized in late winter. Muskoxen conserve the capital of body protein stores for reproductive investment while using income of dietary protein for maintenance functions. We conclude that variation in protein supplies from body stores and the diet explain a large part of the variation in productivity of Arctic ungulates.

Introduction

Animals use various strategies to allocate resources for reproduction in seasonal environments. Reproductive females may rely entirely on stored (capital) or external sources of nutrients (income; Drent and Daan 1980), or, in most cases, a mixture of

[a]Gustine, D. D., P. S. Barboza, and J. P. Lawler. 2010. Dynamics of body protein and the implications for reproduction in captive muskoxen (*Ovibos moschatus*) during winter. Physiological and Biochemical Zoology 83:687-697.

endogenous and exogenous resources to meet the demands of reproduction (Klaassen et al. 2006). The capital available for reproduction includes stores of protein (skeletal muscle) and energy (body lipids, Oftedal 2000).

Body proteins are an important store for N during reproduction (Oftedal 2000, Barboza and Parker 2008). Body protein may serve a role in reproduction in 2 ways: reallocation of maternal proteins (capital) to address the demands of fetal or neonatal growth (Trigg and Topps 1981, Bryant and Smith 1982) and the diversion of dietary proteins (income) to offset the investment of maternal proteins in fetal growth (Barboza and Parker 2008). Marine mammals (Mellish et al. 1999) and some ruminants appear to use muscle proteins as a labile store for reproduction (Chan-McLeod et al. 1995, Gerhart et al. 1996, Barboza and Parker 2008).

Northern ungulates have typically been considered capital breeders (Moen et al. 2006). However, reproductive investment in caribou (*Rangifer tarandus granti*) and reindeer (*R. t. tarandus*) appears to be flexible. *Rangifer* spp. display a marked diversity in behavioral (e.g., Bergerud 1996) and physiological adaptations (Barboza and Parker 2008) to reproducing in northern environments. Alternatively, muskoxen (*Ovibos moschatus*) appear to characterize "classic" adaptations to a capital breeding strategy (Moen et al. 2006). Muskoxen are sedentary, large-bodied grazers, that establish, conserve, and use large body stores to reproduce in austere and uncertain conditions of Arctic and sub-Arctic winters (Klein 1992, Adamczewski et al. 1997, Lawler and White 1997, White et al. 1997, Gunn and Adamczewski 2003).

As capital breeders, reproduction in muskoxen may be constrained by the availability of body protein during gestation. Although the probability of pregnancy is strongly linked to stores of body lipid (White et al. 1997, Adamczewski et al. 1998), the availability of labile body proteins as a store for fetal and early neonatal growth may constitute a nutritional "bottleneck" for muskoxen (White et al. 1989, White et al. 1997). Body stores are established during a short period (6-8 weeks) of replenishment and rapid fattening in late summer and fall (White et al. 1989, Adamczewski et al. 1992) followed by an extended period of demand marked by decreasing forage availability in winter due

to snow cover and the impacts of grazing (Nellemann 1997). In winter, muskoxen rely heavily on body stores (Adamczewski et al. 1995) as well as diets that are low in N and energy (Ihl and Klein 2001, Larter and Nagy 2004). Demands for energy and N increase progressively through late winter for reproductive females as most fetal tissues are deposited in the last trimester and milk production increases after parturition (Oftedal 1985). During periods of prolonged or excessive restrictions in forage in late winter, female muskoxen may allocate protein to maintain their own body tissues rather than depositing protein in offspring [bighorn sheep (*Ovis canadensis*), Festa-Bianchet and Jorgenson 1998, Chan-McLeod et al. 1999, e.g., caribou, Adams 2005].

Isotopes of N have been used to track sources of nutrients allocated towards reproduction (e.g., Hobson 2006). Recent work has employed isotopes of N to determine sources of waste N as well as the allocation of resources during reproduction in female *Rangifer* spp. (Barboza and Parker 2006; 2008). Stores of body N or protein are heavier in ^{15}N than dietary sources of N (Kelly 2000), and, consequently, the principle of mass balance can be used to estimate the extent to which an individual relies on endogenous proteins to meet nutritional requirements (urinary urea, Barboza and Parker 2006) or to produce an offspring (e.g., sources of egg proteins, Hobson et al. 2005). Proportional investments of endogenous resources can be estimated by the isotopic assessment of the tissue(s) involved (e.g., the proportion of maternal N in fetal muscle), or through proxies of tissue reallocation (e.g., proportion of serum amino acid and urea N derived from body N). The circulating pool of amino acids in the blood comprises both non-essential and essential amino acids of endogenous and exogenous origins (Barboza et al. 2009). Similarly, urea N in urine is derived from either endogenous or exogenous proteins (Barboza and Parker 2006). Consequently, the proportions of N in serum amino acids and urinary urea that are derived from body N should be related to reutilization of amino N from body protein. These indices of protein reutilization should increase during late gestation in capital breeders as they reallocate maternal stores of protein to reproduction (e.g., muskoxen in late winter).

We evaluated protein dynamics of captive female muskoxen by measuring body

composition over late gestation (early February to 5 days after calving), the birth masses of their calves, and N isotopes in serum amino acids and urinary urea. We hypothesized that female muskoxen, as capital breeders, rely exclusively on endogenous sources of protein for late gestation and early parturition. Therefore we predicted that pregnant females would lose body protein in late winter whereas non-pregnant controls would maintain or regain stores of body protein. We hypothesized that maternal loss of protein was associated with the development of fetal and uterine tissues. Consequently, we predicted that losses of body protein in pregnant animals would be similar to the protein deposited in reproductive tissues. We hypothesized that pools of N in amino acids and urea in pregnant animals would reflect body protein rather than dietary protein. Therefore we predicted that proportions of amino-N and urea-N that were derived from body protein would be greater in pregnant than non-pregnant females.

Methods

We studied 14 female muskoxen (not pregnant, $n = 9$; pregnant, $n = 5$) in February-June 2007 to assess changes in body composition and isotopic correlates of body condition in blood and urine. No animals lactated during the previous year. Control females were not pregnant in late winter because they were not allowed to breed ($n = 7$) or failed to deliver a calf in spring ($n = 2$). For females that did not deliver a calf in spring, we conducted serum-progesterone assays (Diagnostic Center for Population and Animal Health, Michigan State University, Lansing, MI) of blood samples collected in early February to confirm reproductive status (Rowell et al. 1997); both females that were bred but did not calve were not pregnant in February and were placed in the control group. Not pregnant and pregnant animals with similar body masses were paired at the onset of experiment. All procedures and handling protocols were approved by the Institutional Animal Care and Use Committee (protocol 06-049) at the University of Alaska Fairbanks (UAF). Muskoxen were housed at the Robert G. White Large Animal Research Station (LARS) at UAF (65.074°N, 148.449°W). Ambient temperature at LARS ranged from -37°C in January to +27°C in early June with a total snowfall of 35

cm. Snow cover persisted through mid-April.

Animals were kept in the same enclosure (11.4 ha) and fed a diet of grass hay *ad libitum* (*Bromus* spp.) with a mineral supplement (M ration, Alaska Pet and Garden Anchorage, AK); snow or drinking water was available *ad libitum* throughout the study. Access to natural forages in the paddock was limited, but animals could graze on small amounts of pasture, which was predominantly grass (*Bromus* spp.). The supplement was provided weekly at 35 $g \cdot kg^{-0.75}$ body mass in 2 equal rations (see the common supplement in Peltier and Barboza 2003). To avoid any short-term changes in the urea pool, we withheld supplements for 5 days before sampling blood and urine. Samples of food (hay and supplement) were collected every 4 weeks between 7 February and 5 April, then 5 days after calving (Postcalving, 30 April to 6 June). We collected approximately 50 g of hay during each sampling period. Foods were dried in a forced-air oven at 50°C for >96 h and then ground through a 1 mm screen in a Wiley mill (Arthur Thompson Company, Philadelphia, PA) for subsequent analyses of fiber, ash and N by procedures described in Peltier and Barboza (2003) and in Barboza, Peltier, and Forster (2006).

Blood and urine were sampled on the same days of forage collection. Animals were restrained in a handling chute to withdraw 20 mL of blood from the jugular vein with an 18 gauge x 1.5 inch needle (Becton Dickinson, Franklin Lakes, NJ). Plasma was separated from blood cells in 10 mL tubes containing Na heparin (Becton Dickinson). Blood was allowed to clot in 10 mL tubes without an additive at room temperature before separating serum. Blood samples were centrifuged at 3,000 x *g* at room temperature. Plasma and serum was pipetted into 3.6 mL cryovials (Nalge Nunc International, Rochester, NY) and stored at -20°C. Excess serum was decanted from clotted blood to retain a clot that was mostly red blood cells and fibrin. Drained blood clots were transferred to 14-mL plastic tubes (Falcon, Becton Dickinson) and lyophilized (Freeze Dryer 8, Labconco Corporation, Kansas City, MO).

A disposable ion-exchange column (7090-03, J. T. Baker, Lopatcong Township, NJ) and vacuum manifold (7208-00, J. T. Baker) were used to isolate amino acids from blood serum. Serum proteins were precipitated with sodium tungstate (Na_2WO_4) and

removed by centrifugation at 10,000 x *g* at 10°C (Nolan and Leng 1972). The ion-exchange column was conditioned with methanol (5 mL) and then a binding buffer (5 mL, KH_2PO_4, 0.1 M, pH = 2). Column flows were maintained below 5 $mL \cdot min^{-1}$ for all elutions. Deproteinized samples of 0.5 to 1.5 mL serum were loaded onto individual columns with 5 mL binding buffer. Urea and small peptides were removed by elution from the column. Amino acids were eluted with releasing buffer (5 mL, KH_2PO_4, 0.1 M, pH = 12), collected in 14-mL plastic tubes (Falcon, Becton Dickinson), stored at -20°C, and lyophilized for isotopic analysis.

Individual samples of urine in snow (hereafter referred to as urine) were collected from each animal by moving muskoxen to a snow-covered enclosure (0.45 ha) where voided urine was collected into 100 mL plastic bottles (VWR International, West Chester, PA). Urine was lyophilized and reconstituted to 3.6 mL with distilled water and stored in cryovials (Nalge Nunc International) at -20°C until processing. Urinary urea N was collected by steam distillation (Nolan and Leng 1972, Barboza et al. 1997). We used high performance liquid chromatography (Xue et al. 1988, Barboza and Parker 2006) to isolate and quantify creatinine from urine samples.

Body stores

We measured components of body stores (i.e., total body fat, subcutaneous fat, and body protein) through dilution of body water space and ultrasonography. We measured body mass (1000 to 1530 hrs) on the days of forage and blood sampling with a platform scale (0.5 kg; Tru-Test Model 703, San Antonio, TX). Body water space was estimated with a single dose of tritiated water (^3H_2O; $1 \mu Ci \cdot kg^{-1}$) in 2 sampling sessions: late pregnancy (4-5 February) and Postcalving. Blood was sampled (10 mL) immediately prior to dosing and at 3 and 24 h post-injection. We transferred blood to dry Na heparin tubes (Becton Dickinson) and centrifuged the samples to separate plasma. Plasma was assayed for ^3H_2O by scintillation counting (Beckman LS6000SE, Beckman Coulter, Fullerton, CA) and urea by the diacetyl-monoxime method (Marsh et al. 1965, Peltier et al. 2003). Assumptions and estimates of body water space, corrections for digesta mass

(18.0% of body mass) and water content (88.9% of digesta mass) of digesta, and subsequent estimates of total fat and lean mass were calculated as in Crater and Barboza (2007) with corrections to ingesta-free body mass for the mass of pelage and ash from Adamczewski et al. (1995). Subcutaneous fat at the rump was measured by ultrasonography (Tringa 50S, Esaote Pie Medical, Maastricht, NL; Stephenson et al. 1998) on standing muskoxen (Rombach et al. 2002).

We calculated the absolute and mass-specific rates of change in body fat and protein from the change in total fat and lean mass, respectively, between February and Postcalving. For absolute rates of change ($g \cdot d^{-1}$), we calculated the differences in total fat and lean mass and divided by the number of days between February and Postcalving (87 to 145 d). For mass-specific rates of change in total fat, we divided the difference in total fat between sampling periods by metabolic body mass ($kg^{0.75}$) in February and the number of days the animals were in the study ($g \cdot kg^{-0.75} \cdot d^{-1}$). Energy equivalents for depot fat were estimated at 39.3 $kJ \cdot g^{-1}$ (Blaxter 1989). Lean mass was converted to body protein using the equation from Adamczewski (1995; body protein = 0.207 x lean mass). Change in body protein was the difference between the February and Postcalving estimates of body protein. Changes in body protein were scaled to metabolic body mass in February and divided by the length of time animals were in the study (mg protein·kg body $mass^{-0.75} \cdot d^{-1}$).

We estimated the protein deposited in reproductive tissues from February to Postcalving. Calves were weighed to the nearest 0.1 kg with a platform scale (T-84, Terraillon Corp, Sturtevant, WI) within 12 h of birth. We used relationships between body mass, ingesta-free body mass (IFBM), and body protein of muskox calves to derive the following equation for the protein content of calves:

$$\text{Calf protein (kg)} = \text{body mass (kg)} \times 0.987 \times 0.1959$$

where 0.987 is the proportion of IFBM in the whole body (Knott et al. 2005) and 0.1959 is the proportion of protein in IFBM (Adamczewski et al. 1995). We assumed that the amount of uterine tissue lost during birth was 22% of the birth mass of the calf (Oftedal 1985) and that the protein concentration of uterine tissue was similar to that of the calf

(Barboza and Parker 2008). The protein contents of the calf and uterine tissue were summed to estimate the protein deposited in reproductive tissues. We assumed 80% of fetal investment occurred during the last trimester (Robbins and Robbins 1979) of the 235 d pregnancy (Rowell et al. 1993). The amount of protein in reproductive tissues was scaled to metabolic body mass in February and divided by the length of time animals were in the study (mg protein·kg body mass$^{-0.75}$·d^{-1}).

Isotopic models of protein status

We used isotope ratio mass spectrometry (IRMS; Europa Scientific 20-20 Continuous Flow IRMS interfaced with Europa ANCA-SL elemental analyzer, Europa Scientific, Crewe, UK) to measure enrichment of ^{15}N which was expressed in delta notation (δ) in parts per thousand (‰) against atmospheric N. IRMS was conducted at the Marine Biological Laboratory, Woods Hole, MA or the Forest Soils Laboratory, UAF, Fairbanks, AK. The accuracy of these systems was within 0.39‰ as compared to the $\delta^{15}N$ of peptone from meat (P7750, Sigma-Aldrich Corporation, St. Louis, MO).

We used isotopic ratios of N in serum amino acids and urinary urea to determine sources of N (body or diet) for evaluating maternal allocation of body protein to reproduction (Table 2.1). The proportion of amino acid N derived from body N (*p*-AN) was estimated for free amino acids in blood serum ($\delta^{15}N_{AA}$) using the following equation:

$$p\text{-AN} = \frac{(\delta^{15}N_{AA} - \delta^{15}N_{Diet})}{(\delta^{15}N_{Body} - \delta^{15}N_{Diet})}$$

where $\delta^{15}N_{Diet}$ is the isotopic estimate of the diet (grass hay) and $\delta^{15}N_{Body}$ is the isotopic estimate of body tissue measured in red blood cells. Similarly, the proportion of urea N derived from body N (*p*-UN) was calculated with the following equation from Barboza and Parker (2006):

$$p\text{-UN} = \frac{(\delta^{15}N_{Urea} + \Delta_{Urea} - \delta^{15}N_{Diet})}{(\delta^{15}N_{Body} - \delta^{15}N_{Diet})}$$

where $\delta^{15}N_{Urea}$ is the isotopic estimate of urinary urea N. The Δ_{Urea} term is the discrimination factor for the formation of urinary urea N from dietary N ($\delta^{15}N_{Urea}$ -

$\delta^{15}N_{Diet}$) for animals in positive N balance (i.e., pregnant muskoxen in February: 2.9 ± 0.29‰, $\bar{x} \pm$ SE). We used red blood cells (p-UN_{RBC}) or urinary creatinine (p-$UN_{Creatinine}$) to estimate the $\delta^{15}N_{Body}$ (Table 2.1).

Statistical analyses

We used descriptive statistics and analysis of variance (ANOVA; Zar 1999) to compare initial components of body stores (i.e., depth of rump fat, subcutaneous fat, total fat, and body protein) and ages of females by reproductive status. We used a repeated measures analysis of variance (rmANOVA) to compare reproductive status with the change (%) in body mass, depth of rump fat (cm), and the concentration of plasma urea ($mg \cdot dl^{-1}$) from February to Postcalving. We used the Mann-Whitney U-test to evaluate the changes (%) in total fat and lean mass from February to Postcalving (as estimated by body composition in February and Postcalving) by reproductive status and the Wilcoxon sign-rank (Siegel 1956) test to determine whether changes in total fat and body protein for not pregnant and pregnant muskoxen were different from zero. We used ANOVA to examine the effect of reproduction on the absolute and mass-specific rates of change in fat and protein and compared those rates with zero by using t-tests. We used linear regression to examine relationships between the change in body stores (i.e., proportion or rate of change in depth of rump fat, total fat, and body protein) and the initial size of the store. Analysis of variance was used to examine the $\delta^{15}N$ of hay by period while rmANOVA was used to examine the $\delta^{15}N$ of red blood cells, urinary creatinine, serum amino acids, urinary urea, p-AN, and p-UN (as estimated from red blood cells as the proxy for $\delta^{15}N_{Body}$) by reproductive status and period. We used Bonferroni's correction to alpha for all multiple comparisons. We used linear regression and correlation coefficients to evaluate the predictions of p-UN derived from proxies of $\delta^{15}N_{Body}$ (red blood cells and urinary creatinine; Table 2.1) for February, March, and April. We used confidence intervals (95%) of the slopes to compare the linear relationship of p-UN_{RBC} (y) and the p-$UN_{Creatinine}$ (x) by period with unity.

All statistics were analyzed with Stata 9.2 (StataCorp, College Station, TX). We

used a Shapiro-Francia test to assess the assumption of normality for all comparisons. Significance of all tests was defined at $\alpha = 0.050$ and, unless specified otherwise, results are reported as means ($\bar{x}$) ± SE.

Results

The grass hay provided a consistent diet that was moderately low in N (1.3 ± 0.06 % DM) and high in fiber (63.0 ± 1.85% neutral detergent fiber; 35.6 ± 0.73% acid detergent fiber) with a moderate concentration of ash (6.4 ± 1.51% DM). The supplement was 2.6% N and low in fiber (24.1% neutral detergent fiber; 12.0% acid detergent fiber; 6.9% ash; Peltier and Barboza 2003).

Body stores

Not pregnant and pregnant muskoxen displayed marked changes in body stores from February to Postcalving (**APPENDIX A**: Table A.1). Pregnant muskoxen were younger and had more lean mass in February than the non-pregnant controls (Table 2.2). All muskoxen lost body mass and rump fat (Fig. 2.1) from February to Postcalving. There was a significant interaction between period and reproductive status as pregnant muskoxen lost more body mass than non-pregnant females between April and Postcalving (Fig. 2.1). The concentration of urea in plasma did not vary by reproductive status and increased in all muskoxen from February to Postcalving (Fig 2.2).

Muskoxen lost body fat from February to Postcalving (-24 ± 6.1%; Mann-Whitney *U*-test, reproductive status, $z = 0.20$, $P = 0.842$; Wilcoxon sign-rank test, different from zero, both $z < -2.03$, both $P < 0.043$). Similarly, absolute and mass-specific changes in fat (-129 ± 27.9 $g \cdot d^{-1}$; -2.2 ± 0.48 $g\ kg^{-0.75} \cdot d^{-1}$) and, subsequently, energy from fat depots (-5,060 ± 1095.6 $kJ \cdot d^{-1}$; -85± 18.8 $kJ\ kg^{-0.75} \cdot d^{-1}$) were less than zero (*t*-tests, both $t < -3.01$, both $P < 0.040$) and did not vary with reproductive status (ANOVA, both $F_{1, 12} < 0.13$, both $P > 0.851$). Stores of body fat in February (as indexed by depth of rump fat and total body fat) were not related to the amount of fat lost (linear regression, both $r^2 < 0.109$; all $P > 0.248$).

Unlike fat, the changes in body protein varied with reproductive status. Pregnant

muskoxen lost body protein from February to Postcalving (-6.1 ± 2.06%; Mann-Whitney *U*-test, reproductive status, $z = 2.07$, $P = 0.039$; Wilcoxon sign-rank test, different from zero, $z = -2.02$, $P = 0.043$) while individuals that were not pregnant appeared to maintain body protein (6.2 ± 4.35%; Wilcoxon sign-rank test, $z = 1.24$, $P = 0.214$). Similarly, absolute changes in body protein also varied with reproductive status (ANOVA, $F_{1, 12} = 6.93$, $P = 0.022$): pregnant muskoxen lost body protein (-15.7 ± 4.30 $g \cdot d^{-1}$; *t*-test, $t_{one\text{-}tailed} = -3.65$, $P = 0.011$) while animals that were not pregnant maintained body protein throughout winter (11.2 ± 11.12 $g \cdot d^{-1}$; $t = 1.57$, $P = 0.155$). Body protein in February was inversely related to the change in body protein from February to Postcalving (linear regression, $r^2 = 0.369$; $P = 0.021$; -0.77 ± 0.29, slope ± SE; Fig. 2.3).

Estimates of protein status varied with reproductive status (*t*-test, $t_{one\text{-}tailed} = 2.50$, $P = 0.014$). Muskoxen that were not pregnant maintained body protein albeit with high variation among individuals (190 ± 124.6 mg protein·$kg^{-0.75} \cdot d^{-1}$; *t*-test, $t = 1.53$, $P = 0.165$), while pregnant animals lost protein throughout late gestation (-255 ± 71.5; $t_{one\text{-}tailed} = -3.57$, $P = 0.012$). The body masses of pregnant muskoxen at parturition were 210.3 ± 25.9 kg. Five calves (9.96 ± 0.91 kg) were born on 13 May ± 7.3 d with 2 of those calves dying at birth (i.e., still birth and malpresentation). The deposition of protein in calves and uterine tissues during gestation (319 ± 33.4 mg protein·$kg^{-0.75} \cdot d^{-1}$) was similar to the loss of body protein in pregnant muskoxen (*t*-test, $t = -0.682$, $P = 0.533$).

Isotopic models of protein status

The components of the isotopic models varied in their response to time and (or) reproductive status (**APPENDIX A**: Table A.2). The diet of grass hay ($\delta^{15}N_{Diet}$) appeared to change with period (ANOVA, $F_{2, 6} = 6.39$, $P = 0.033$) from 1.0 ± 0.10‰ in February to 0.6 ± 0.20‰ in Postcalving, but when Bonferroni's correction was applied ($\alpha = 0.017$), pair-wise comparisons of the monthly samples of hay were not different (all $P > 0.047$). We therefore used the average $\delta^{15}N_{Diet}$ by period for all subsequent analyses. The $\delta^{15}N$ of the mineral supplement (1.7 ± 0.15‰) was similar across periods ($F_{3, 4} = 1.01$, $P = 0.480$). The isotopic proxies of body tissue in muskoxen ($\delta^{15}N_{RBC}$ and $\delta^{15}N_{Creatinine}$)

changed across periods (rmANOVA, both $F > 5.36$, both $P < 0.013$; Fig. 2.4a) but did not vary with reproductive status (both $F < 4.22$, both $P > 0.060$). There was an interaction between the period and reproductive status for $\delta^{15}N_{RBC}$ ($F = 5.69$, $P = 0.003$) but not for $\delta^{15}N_{Creatinine}$ ($F = 0.62$, $P = 0.544$). The $\delta^{15}N_{AA}$ and $\delta^{15}N_{Urea}$ did not vary from February to Postcalving (all $F < 4.32$, all $P > 0.059$; Fig. 2.4b).

Both the isotopic models of protein status (i.e., *p*-AN and *p*-UN) did not vary with reproductive status, while only the *p*-UN increased significantly across periods (Fig. 2.5). Unfortunately we could not collect urine samples at Postcalving because there was no snow, and, so we could not estimate *p*-UN for this period. Estimates of *p*-UN that were derived from the $\delta^{15}N$ of red blood cells were closely correlated with those from urinary creatinine for each period (February, $r = 0.99$; March, $r = 1.00$; April, $r = 0.92$) and did not differ from unity in February (0.98 to 1.20, 95% CI) and April (0.57 to 1.01) but were greater than unity in March (1.10 to 1.27).

Discussion

Body stores

All muskoxen lost body mass and fat over the winter while pregnant muskoxen lost body protein in late gestation. Body masses (189-274 kg, range) were typical of adult female muskoxen in captive herds (218-250 kg, Adamczewski et al. 1992), and exceeded the body masses of free-ranging muskoxen (e.g., 150-190 kg, Adamczewski et al. 1997). As observed in wild muskoxen in winter (Adamczewski et al. 1997), both reproductive classes of muskoxen lost body mass, with almost all of those losses occurring in late winter (Fig. 2.1a). Captive conditions that provided food *ad libitum* allowed females to enter winter in better body condition than those in the wild and to regain mass more quickly in late winter especially when females were not pregnant. In our study, captive females lost less mass (6-12% of body mass from February to Postcalving) than females in the wild on Victoria Island (14-27%, November to April; Adamczewski et al. 1997) and Greenland (September to April, 26%; Thing et al. 1987).

Initial stores of subcutaneous fat in captive muskoxen were generally similar to

wild muskoxen, but captive muskoxen lost less subcutaneous fat than has been reported for wild muskoxen. Losses of subcutaneous fat from early winter to parturition approached (Thing et al. 1987) or exceeded 50% in wild muskoxen (Adamczewski et al. 1997) while females at LARS lost only 22-28% of their subcutaneous fat (Fig. 2.1). Pregnant and non-pregnant muskoxen at LARS had large stores of body lipid. Total fat at Postcalving (~44-47 kg) was similar to the annual maxima of non-lactating, wild muskoxen (~45-47 kg; Adamczewski et al. 1997). The role of fat stores has clear implications to survival and reproduction in muskoxen (White et al. 1997). Energy-conserving behaviors (Jingfors 1982), a low metabolic rate (Lawler and White 1997), and large stores of lipids enable muskoxen to meet a large proportion of their energetic needs from body fat during winter (Adamczewski 1995). In this study, large fat stores indicated that energy was unlikely to limit reproduction in these captive animals. Energy released from fat was equivalent to 25 ± 5.0% of the energy expended at rest (lying and standing) by fasting muskoxen (370 $kJ \cdot kg^{-0.75} \cdot d^{-1}$; Lawler and White 1997).

As predicted, reproductive females lost body protein in late winter even though they were in excellent body condition and provided with hay *ad libitum*. The amount of body protein in pregnant muskoxen at LARS in February (Table 2.1) was similar to wild muskoxen in November (pregnant = 25.6 ± 0.3 kg). All reproductive classes of adult females in wild muskoxen lost body protein over winter (20-31%, range; Adamczewski et al. 1997) so that body protein levels were similar between reproductive and non-reproductive females at the end of winter (Adamczewski et al. 1997). However, for muskoxen at LARS, only pregnant animals lost body protein (6%) while 6 of 9 non-reproductive muskoxen gained body protein (Fig. 2.3). In wild muskoxen, most protein loss occurs in reproductive females during late winter (Adamczewski et al. 1997) and early lactation (10-20 d; White et al. 1989). It is likely that the highest loss of maternal protein in captive muskoxen coincided with the highest amount of mass loss in late gestation (Fig. 2.1). It is unlikely that body protein was used as an energy substrate in captive females because loss of body mass was strongly correlated with fat loss ($n = 5$, $r = 0.96$) and because maternal protein loss was equivalent to the estimated deposition of

protein in the calf and uterine tissues.

The amount of body protein in muskoxen in February appeared to influence the trajectory of that store in late winter. Lighter, non-pregnant animals maintained or restored body protein, while heavier, pregnant muskoxen lost body protein in late winter (Fig. 2.3). The relationship suggests that, as in caribou (Gerhart et al. 1997), lighter, non-reproductive muskoxen may have the capacity to recover body protein in winter. For domestic animals given sub-maintenance diets, a similar relationship has been observed for body lipids (e.g., smaller animals lost less fat, Chilliard et al. 2000), however, we did not detect this relationship for body fat. Although we were limited by a small sample size, we did not detect that larger daily "investments" of body protein translated into larger calves (e.g., caribou, Allaye-Chan 1991).

Muskoxen have small calves when compared to other ungulates of similar body mass (Robbins and Robbins 1979). Indeed, calves at LARS demonstrated a markedly low investment in fetal growth relative to maternal mass (kg) at parturition: the predicted birth mass [maternal mass (kg) 0.7933 x 0.2143; Robbins and Robbins 1979] of these calves was 15.3 ± 0.56 kg, which is 5 kg greater than the actual birth masses. Low maternal investment in fetal growth is combined with a conservative use of maternal protein because the rates of protein loss in pregnant muskoxen were similar to the amount of protein deposited in reproductive tissues. This similarity in protein "lost" from body tissue and "invested" in reproductive tissue epitomizes a capital breeder and supports the role of body protein as a labile store for reproduction.

Isotopic routing of N

Amino N was oxidized and reutilized between April and Postcalving because the loss of body protein in pregnant muskoxen during late gestation was accompanied by an increase in plasma urea concentration (Fig. 2.2) and enrichment of red blood cells in $\delta^{15}N$ (Fig. 2.4a). However, $\delta^{15}N_{AA}$ (Fig. 2.4b) and *p*-AN (Fig. 2.5a) were not altered by the slow loss of body protein, which suggests that body tissues were probably maintained with stored protein. These patterns of enrichment in $\delta^{15}N$ indicate that even though

muskoxen had not started to restore body protein, pregnant muskoxen were well within their ability to maintain their tissues by reutilizing amino acids released from mobilized protein. Pregnant muskoxen may have been using dietary N to address the demands of tissue maintenance while stores of body protein were allocated for reproduction (Barboza and Parker 2006; 2008).

The high $\delta^{15}N$ of amino acids resulted in high estimates of *p*-AN (>0.40; Fig. 2.5a) that indicated a large part of the circulating pool of amino acids was derived from body protein. The mobilization of 6% of body protein over the last trimester of gestation (~78 d) may not have been sufficient to further enrich an amino acid pool that was already dominated by endogenous N. However, the pool of amino acids should respond to changes in dietary N intake because the turnover of free amino acids in the blood is faster than that of protein in tissues (Waterlow 1999). A consistent *p*-AN in both reproductive classes of muskoxen is consistent with low food intakes and slow influxes of N in muskoxen through late winter (Peltier and Barboza 2003). There are two factors, however, that may have affected our absolute estimates of *p*-AN: the potential enrichment of dietary N by rumen microbes and the lack of a discrimination factor in estimating *p*-AN. Approximately 50% of the amino acids absorbed by ruminants are derived from microbial protein (Agricultural Food Research Council 1992). Although poorly understood, it appears that modification of dietary ^{15}N by ruminal microbes is likely low (Sutoh et al. 1987) and the enrichment or depletion of $\delta^{15}N_{Diet}$ probably depends on the flux and degradability of N in the rumen (Leng and Nolan 1984, Barboza and Parker 2006, Karasov and Martinez del Rio 2007). Similarly, a lack of a discrimination factor for the formation of amino acids from dietary N for animals in positive N balance (i.e., Δ as in model to estimate *p*-UN) would affect the absolute estimates of *p*-AN. We estimated Δ for urea N because other work has used this metric to estimate N balance in reindeer (Barboza and Parker 2006). Unless the discrimination factor varied with protein demand, any discrimination factor for *p*-AN would alter the absolute estimate but would not affect the comparison between groups. Forthcoming research on the *p*-AN in wintering muskoxen will improve our estimates of N

discrimination between diet and serum amino acids.

Ecological implications

Variance in protein supply from body stores and the diet may explain some of the high variance in reproductive parameters (i.e., pregnancy and calving dates) observed in wild muskoxen. Pregnancy rates for muskox populations are relatively low for adult ungulates (35-73%, Adamczewski et al. 1997), with reproductive pauses possibly common, even in growing populations (Reynolds 2001). The ability to conceive appears tightly linked with levels of fatness in muskoxen (White et al. 1989, Adamczewski et al. 1997, White et al. 1997). The capacity to carry the fetus to term may depend on the sources and availability of dietary proteins for maintenance of body proteins, which, in turn, would affect the amount of capital available for reproductive investment. Muskoxen are apparently unique among ungulates because early luteal regression (10-14 weeks) and reduction in progesterone production at the onset of the last trimester of gestation (20-22 weeks) may enable pregnant females to terminate pregnancies through embryonic mortality or mid-term abortions (Rowell et al. 1993). Although it is not clear, this mechanism may be nutritionally mediated (Rowell et al. 1997) by the availability of exogenous resources for maintenance of tissues and endogenous stores for reproduction.

Similarly, dates of calving are highly asynchronous among populations of muskoxen as females tend to calve from mid-April to mid-June (Tener 1965, Rowell et al. 1993, Reynolds 2001). Timing of birth depends upon both date of conception and gestation length (Adams and Dale 1998). Conception and estrus may be determined by body mass that mainly reflects the store of energy in fat whereas gestation may depend upon both fat and protein reserves. If gestation length in wild muskoxen is flexible (Rowell et al. 1993), as it is in bison (*Bison bison*, Berger 1992) and reindeer (Mysterud et al. 2009), muskoxen may be able to alter gestation length to offset the costs of fetal development on stored capital and possibly delay lactation to better coincide with seasonal plant growth.

The capital-income approach towards reproduction (Drent and Daan 1980) is a

continuum of solutions to balance the nutrient demands of survival and reproduction (Klaassen et al. 2006, Barboza et al. 2009). For wild populations of muskoxen, wide variation in the annual availability of forage (Gray 1987) may affect the degree to which reproductive females depend on stores to support reproduction (White et al. 1989, Oftedal 2000). Indeed, in reindeer, winter conditions tend to have unbalanced effects on the resources available for reproduction, as harsh conditions have stronger effects on the allocation of body mass to reproduction than mild or average winters (Adams 2005, Bårdsen et al. 2008). Our conditions were apparently ideal for reproductive muskoxen, in that females could rely exclusively on dietary resources for maintenance and on stored proteins for reproduction. In wild muskoxen, however, dietary constraints in late winter may be more common (Gray 1987), so animals rely heavily on endogenous reserves for both survival and reproduction. In less favorable years, environmental conditions that reduce the accretion or increase the catabolism of body stores will directly affect the availability of body protein as a store for reproduction. Reproductive muskoxen, therefore become obligated to catabolize body lipids and proteins to maintain homeostasis, and, if stores are available, complete gestation and initiate lactation. Consequently, severe winters coupled with short growing seasons may limit or eliminate the production of calves (Gray 1987, Reynolds 2001). A conservative approach to reproduction enables individuals to take advantage of mild winter conditions, offset the reliance of early reproduction on body stores, and may partially explain some variance in the observed demographic parameters (e.g., pregnancy rates, timing of parturition, and calf productivity) of wild populations.

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Table 2.1. The parameters of isotopic models to estimate protein status as well as definition of terms, source material, and the period the parameter was estimated for not pregnant and pregnant captive muskoxen, Fairbanks, AK, 2007.

Parameter of isotopic models	Definition	Source	Period sampled or estimated			
			February	March	April	Postcalving
$\delta^{15}N_{Diet}$[a]	Dietary N	Forage samples	X	X	X	X
$\delta^{15}N_{AA}$[a]	Free amino acids in serum	Whole blood	X			X
$\delta^{15}N_{Body}$[a]	Red blood cells	Whole blood	X	X	X	X
$\delta^{15}N_{Body}$[b]	Creatinine	Urine in snow	X	X	X	
$\delta^{15}N_{Urea}$[a]	Urea	Urine in snow	X	X	X	
p-AN[c]	Proportion of amino acid N derived from body N	Derived	X			X
p-UN_{RBC}[c]	Proportion of urea N derived from body N as estimated from red blood cells to determine $\delta^{15}N_{Body}$	Derived	X	X	X	X
p-$UN_{Creatinine}$[c]	Proportion of urea N derived from body N as estimated from urinary creatinine to determine $\delta^{15}N_{Body}$	Derived	X	X	X	

[a]Measured directly through isotope ratio mass spectrometry.

[b]Derived from the linear relationship of $\delta^{15}N$ of red blood cells on $\delta^{15}N_{Creatinine}$ for captive muskoxen, reindeer, and caribou [R. Parsley and P. Barboza, unpublished data; $\delta^{15}N_{Body} = (\delta^{15}N_{Creatinine} \times 0.573) + 5.642$; $n = 40$, $r^2 = 0.672$, standard error of estimate = 0.733].

[c]See *Isotopic models of protein status* in **Methods**.

Table 2.2. The age and estimates of the body components of captive female muskoxen ($\bar{x} \pm$ SE) by reproductive status at the beginning of the experiment (4-5 February).

Reproductive Status	*n*	Age (y)	Body mass (kg)	Depth of rump fat (cm)	Total fat[a] (kg)	Body protein (kg)[ab]
Not pregnant	9	13.7 ± 1.0	227.1 ± 9.0	3.65 ± 0.51	59.3 ± 6.5	22.8 ± 0.6
Pregnant	5	7.8 ± 1.3	245.9 ± 9.7	3.96 ± 0.43	61.4 ± 8.4	25.3 ± 0.8
ANOVA[c]		***P* = 0.004**	*P* = 0.207	*P* = 0.669	*P* = 0.845	***P* = 0.031**

[a]We used the dilution of the body water pool with tritiated water to estimate body composition (Crater and Barboza 2007).

[b]We assumed that lean mass (kg) was 20.7% protein (Adamczewski 1995).

[c]Analysis of variance (ANOVA) was used to compare the means by reproductive status.

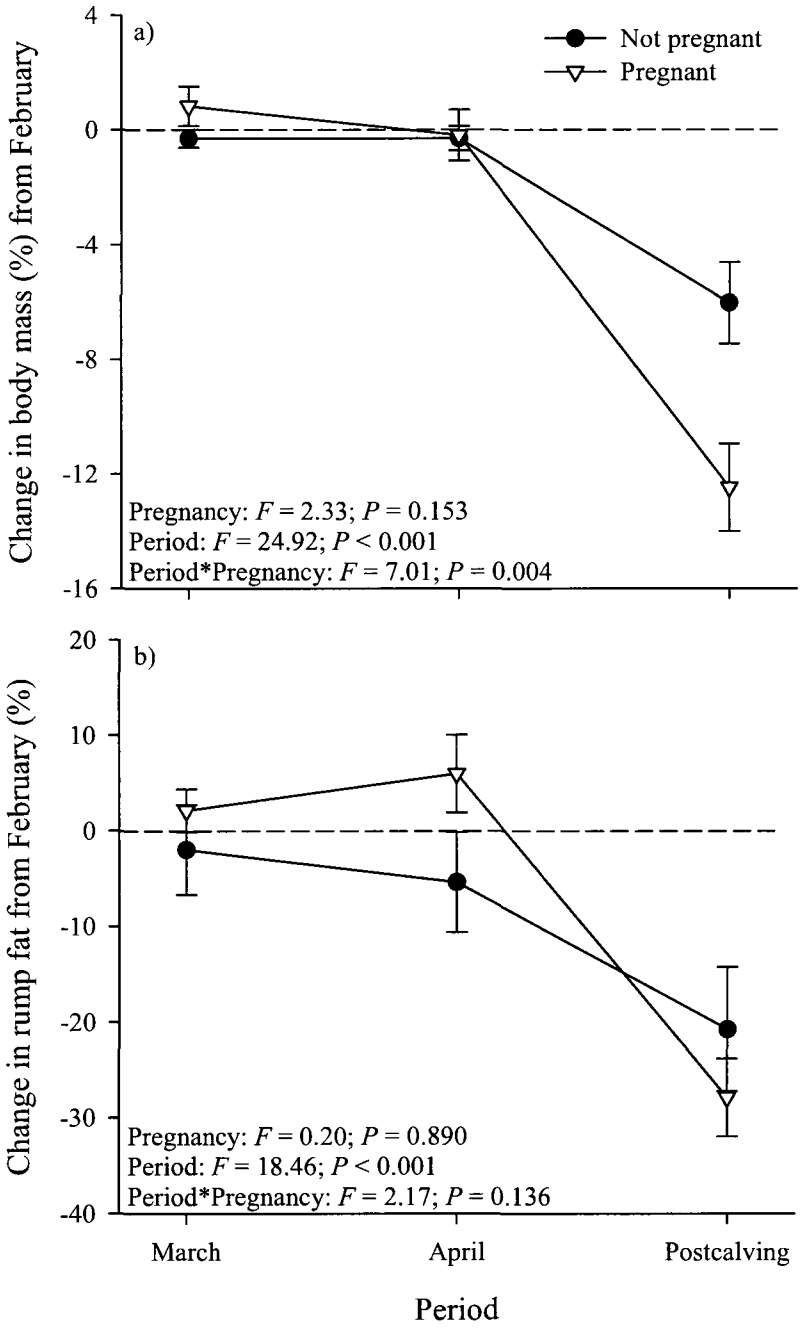

Figure 2.1. The percent change ($\bar{x} \pm$ SE) in a) body mass and b) depth of rump fat from February to Postcalving for pregnant and not pregnant muskoxen in captivity, Fairbanks, AK, 2007. Repeated measures analysis of variance was used to examine the effects and interaction of pregnancy and month by period.

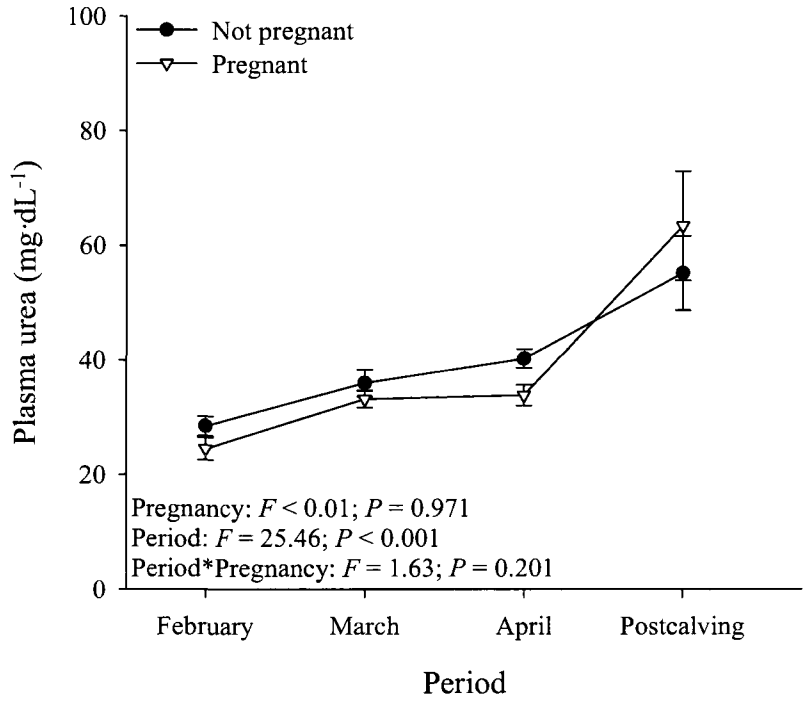

Figure 2.2. The concentration of urea in blood plasma ($mg \cdot dL^{-1}$) for pregnant and not pregnant muskoxen from February to Postcalving, Fairbanks, AK, 2007.

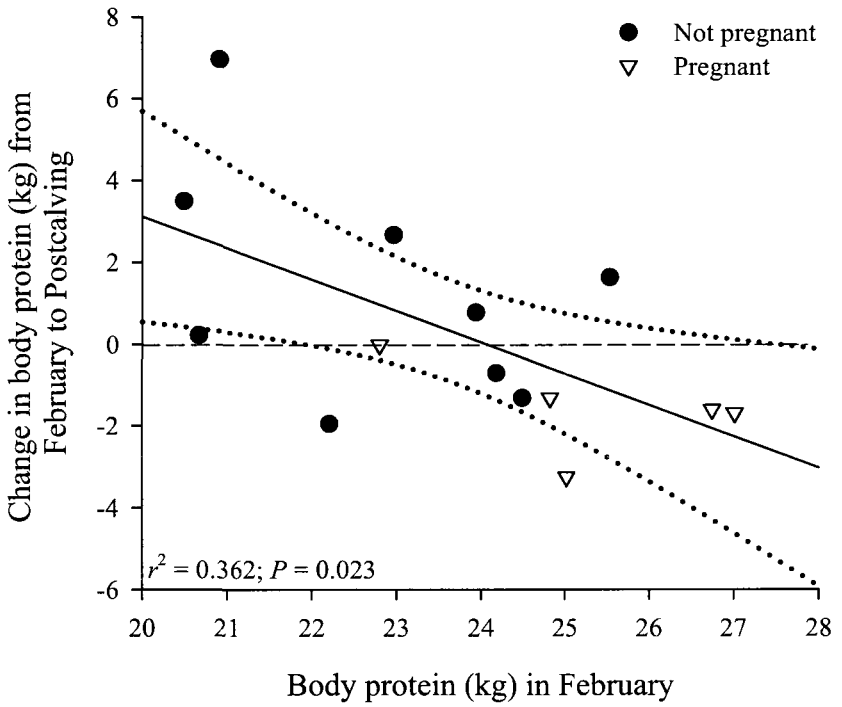

Figure 2.3. The relationship between body protein (kg) in February and the change in body protein from February to Postcalving for pregnant and not pregnant muskoxen in captivity, Fairbanks, AK, 2007; dotted lines indicate the 95% confidence interval for the regression line.

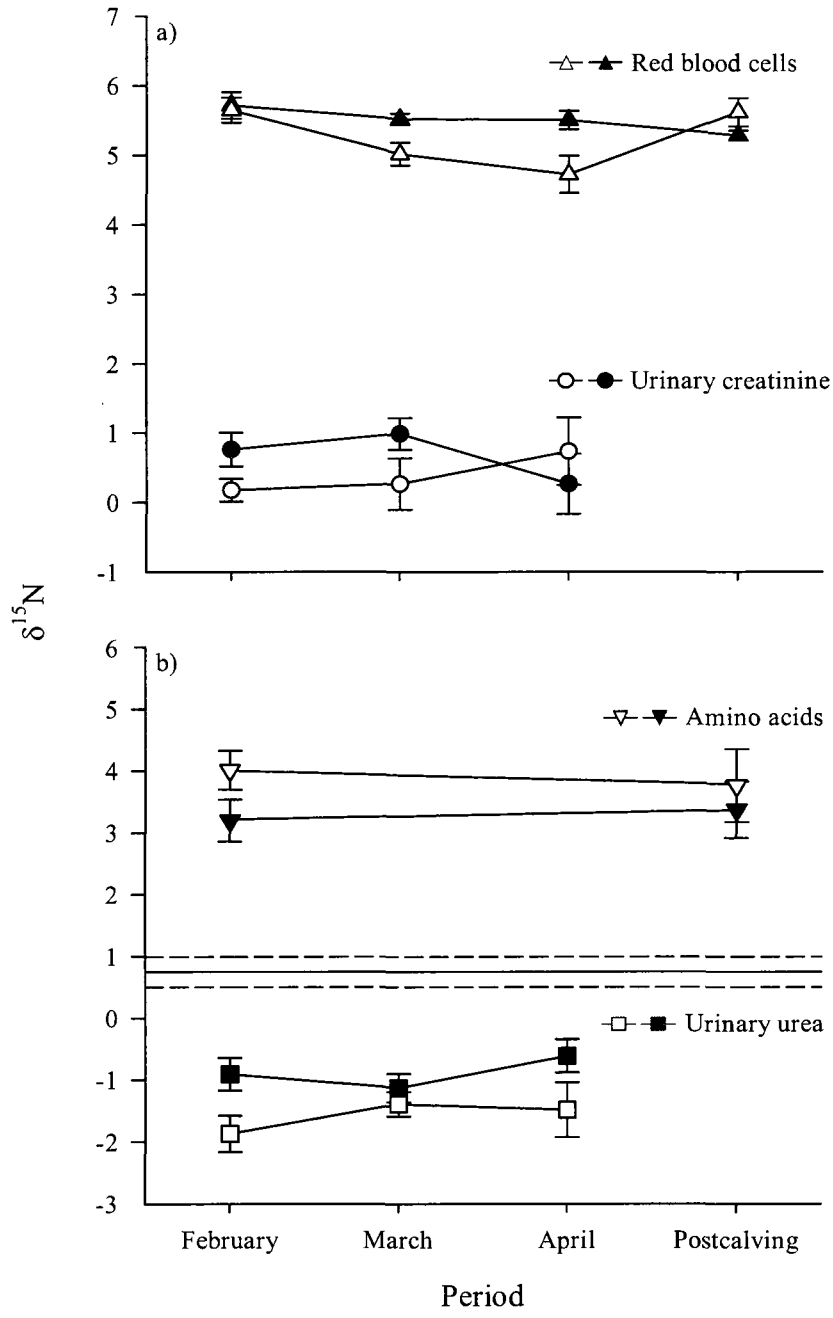

Figure 2.4. The isotopic ($\delta^{15}N$) signatures ($\bar{x} \pm$ SE) of a) red blood cells (triangles), urinary creatinine (circles), b) serum amino acids (inverted triangles), urinary urea (squares), and diet (solid line ± SD) by period for pregnant (open symbols) and not pregnant (closed symbols) captive muskoxen, Fairbanks, AK, 2007.

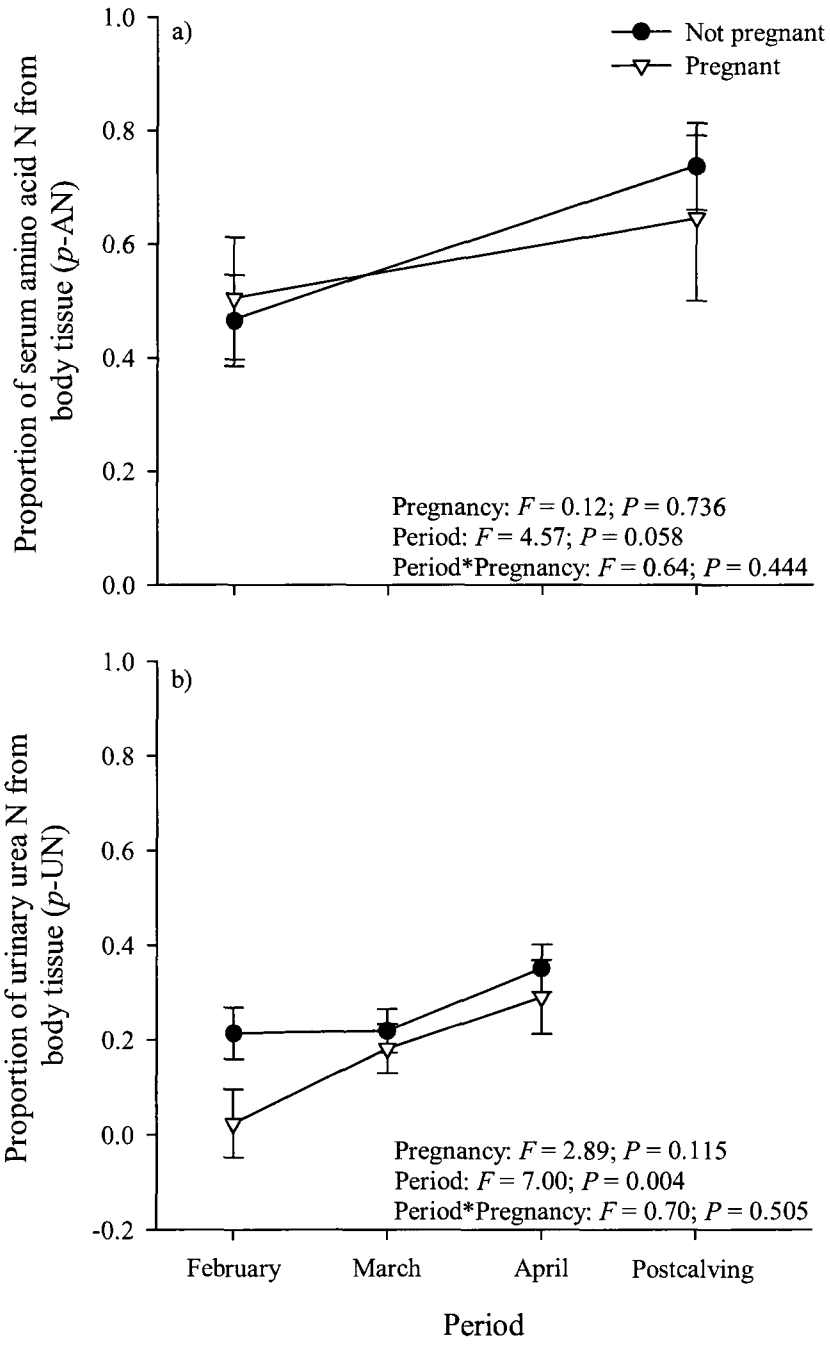

Figure 2.5. The proportions of a) serum amino acid and b) urea N derived from body N ($\bar{x} \pm$ SE) in captive female muskoxen by period and reproductive status as estimated by isotopic ($\delta^{15}N$) proxies of body protein (red blood cells), diet (grass hay), amino acids in the blood serum, and urinary urea.

CHAPTER 3 - CHARACTERISTICS OF FORAGING SITES AND PROTEIN STATUS IN WINTERING MUSKOXEN: INSIGHTS FROM ISOTOPES OF NITROGEN[a]

Abstract

Identifying links between nutritional condition of individuals and population trajectories greatly enhances our understanding of the ecology, conservation, and management of wildlife. For northern ungulates, the potential impacts of a changing climate to populations are predicted to be nutritionally mediated through an increase in the severity and variance in winter conditions. Foraging conditions and the availability of body protein as a store for reproduction in late winter may constrain productivity in muskoxen (*Ovibos moschatus*), yet the link between characteristics of wintering habitats and protein status has not been established for a wild ungulate. We used a non-invasive proxy of protein status derived from isotopes of N in excreta to evaluate the influence of winter habitats on the protein status of muskoxen in 3 populations in Alaska (2005-2008). Multiple regression and an information-theoretic approach were used to compare models that evaluated the influence of population, year, and characteristics of foraging sites (components of diet and physiography) on protein status for groups of muskoxen. The observed variance in protein status among groups of muskoxen across populations and years was partially explained (45%) by local foraging conditions that affected forage availability. Protein status improved for groups of muskoxen as the amount of graminoids in the diet increased (-0.430 ± 0.31, $\beta \pm 95CI$) and elevation of foraging sites decreased (0.824 ± 0.67). Resources available for reproduction in muskoxen are highly dependent upon demographic, environmental, and physiographic constraints that affect forage availability in winter. Due to their very sedentary nature, muskoxen are highly susceptible to localized foraging conditions; therefore, the spatial variance in resource availability may exert a strong effect on productivity. Consequently, accounting for

[a]Gustine, D. D., P. S. Barboza, J. P. Lawler, S. M. Arthur, B. S. Shults, K. Persons, and L. G. Adams. Characteristics of foraging sites and protein status in wintering muskoxen: insights from isotopes of nitrogen. Oikos: *in review*.

climate-topography effects at multiple scales when predicting the potential impacts of climatic shifts on population trajectories of muskoxen is critical.

Introduction

Conservation and management of wildlife depends upon our understanding of the link between the physiology of individuals and the vital rates of their population. Models of population growth in ungulates typically include the effects of intra-specific competition and changes in resource availability and nutritional limitation on reproduction and survival (e.g., Caughley 1970, Clutton-Brock 1982, McCullough 2002). However, nutritional contributions to population changes are often obscured by time-lags and interactions between density-dependent and density-independent factors (Jacobsen et al. 2004, Wang et al. 2006, Stephens et al. 2009). Nonetheless, it is imperative that we increase our understanding of the nutritional contributions to population changes of ungulates, particularly at high latitudes where the rate of environmental change is greatest (Walther et al. 2002).

Some of the potential impacts of a changing climate on populations of northern ungulates are nutritionally mediated through intraspecific competition and variance in environmental conditions in winter that limit forage abundance (Forchhammer et al. 2002, Tyler et al. 2008). The effects of adverse environmental conditions are magnified for animals restricted to small wintering areas or at high densities (Coulson et al. 2000, Larter and Nagy 2001b). Restrictions in forage availability in late winter increase the reliance of reproductive females on stores of energy and protein for survival, and, consequently, less endogenous proteins are available for reproduction. Availability of body proteins are a nutritional constraint for reproductive females as offspring are derived primarily from maternal stores (Barboza and Parker 2008, Gustine et al. 2010). Indeed, sizes or investments of maternal proteins are strongly correlated with protein content of offspring (Allaye-Chan 1991). Consequently, foraging conditions in winter can affect the amount of body stores available to invest in reproduction, and, therefore, affect birth mass (Adams 2005), survival (Skogland 1990), and recruitment of offspring

(Adams et al. 1995, Hegel et al. 2010).

Recently, a non-invasive, isotopic technique was developed to assess the protein status (i.e., gains or losses of body proteins) of northern ungulates in late winter (Barboza and Parker 2006). Isotopic ratios of N (δ; Gannes et al. 1997) in excreta can be used to assess the endogenous and exogenous contributions of N in urinary urea. Body proteins have a higher $\delta^{15}N$ than dietary sources of protein (Kelly 2000), therefore, an increase in the catabolism of body proteins results in an enrichment of urinary urea and, consequently, an increase in the proportion of urinary urea N derived from body N (*p*-UN). This isotopic approach has been applied to captive reindeer (*Rangifer tarandus*; Barboza and Parker 2006) and muskoxen (*O. moschatus*; Gustine et al. 2010) as well as semi-captive caribou (*R. tarandus*; Gustine et al., *in press*), but has not been used to estimate the protein status of populations of wild muskoxen.

Muskoxen are large-bodied grazers (Hofmann 2000) that have simple diets of primarily graminoids (mainly sedges such as *Carex* spp. and *Eriophorum* spp.) and willows (*Salix* spp.) in winter (Ihl and Klein 2001, Larter and Nagy 2004). In the winter, muskoxen exhibit high site fidelity (Jingfors 1982, Nellemann 1998) and are typically confined to small areas (Klein et al. 1993, Ihl 2007). Physiographic and vegetative characteristics of wintering sites are, therefore, strong determinants of forage availability as snow, wind, and topography affect access to forage (e.g., Schaefer and Messier 1995a, Nellemann 1997, Nellemann and Reynolds 1997, Ihl 2007). Graminoids become less available throughout winter as competition for snow-free areas increases (Larter and Nagy 2004) and if the formation of ice layers renders forages unavailable (Parker et al. 1975, Forchhammer and Boertmann 1993). Consequently, groups of muskoxen concentrated in small wintering areas (Klein 1992) are predicted to expand dietary breadth to include less preferred forages (e.g., mosses, Ihl 2010), and may rely more heavily upon body stores to meet demands for energy and protein for survival and reproductive investment. The impacts of herbivory and forage abundance in the winter on the availability of body stores, therefore, may be constraining factors in the productivity of muskoxen populations (Forchhammer et al. 2002).

We present the first application of a non-invasive, isotopic approach to estimate protein status in wild muskoxen. The protein status of groups of muskoxen was examined in relation to the characteristics of wintering sites for 3 populations of muskoxen. We collected samples of recently voided urine and feces in snow to estimate composition and diversity of the diet and protein status. Spatial data and a geographic information system (GIS) were used to estimate physiographic features of wintering locations. The existing literature was used to construct an ecologically plausible set of models that included population and year to explain the observed variance in protein status among groups of muskoxen. We predicted that effects of population or year would reflect a response to demographic (e.g., density) or environmental (e.g., winter severity) constraints, while factors associated with forage availability at smaller scales would be more apparent if proxies of localized foraging conditions were better correlates of protein status.

Methods

Muskoxen populations and study areas

In Alaska, muskoxen were extirpated in the late 19th century, but reintroduction efforts throughout the 20th century established 5 populations (Lent 1998): 2 populations in the southwest and 3 in the north [North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP)]. The NS population is currently stable (~200) but underwent a rapid decline (1995-2005), the causes of which are unclear (S. Arthur, unpublished data). Minimum count data from the CT groups (~300) also suggests this population may be undergoing a decline (Dau 2007, B. Shults, unpublished data). Conversely, the SP is the largest population of muskoxen in the state (~3,000) and is still growing, although at a reduced rate with high spatial variation in productivity and increased observations of dispersal (Gorn and Persons 2007).

We sampled groups of muskoxen along the Sagavanirktok River and on the coastline of Prudhoe Bay on the northern coastal plain of Alaska (NS). In western Alaska, we collected samples from groups near Cape Krusenstern (CT), and throughout

the western portion of the Seward Peninsula (SP; Fig. 3.1). The vegetative associations for the ranges of the NS (Reynolds 1998), CT (Ihl 2010), and SP (Rupp et al. 2000, Ihl and Klein 2001) populations have been described at length elsewhere.

Sample collection and processing

We collected samples of excreta from sites used by 3 populations of muskoxen in late winter (Table 3.1). Sites were the fundamental sampling unit for all analyses; the terms site and group of muskoxen are used interchangeably throughout. Groups of muskoxen were initially located with fixed-wing aircraft. We approached groups by foot, snow machine, or helicopter. Animals were counted using binoculars and spotting scopes. The approximate center of each site was marked with a global positioning system. Recently voided urine in snow (urine) and feces was collected from the surface layer of snow or ice across the linear extents of each site (~50-200 m). We collected discrete defecations or urinations and assumed that samples were from separate individuals. Samples of urine (approx. 100 ml) and feces (approx. 15 g) were collected into plastic bottles or bags with leak-proof seals. We used a small axe, knife, or the collection bottle or bag to assist in collecting the most concentrated portion of each urine sample. Collection tools were cleaned with fresh snow and dried after each collection. Samples were stored at -20°C until processing. We lyophilized the urine samples to concentrate metabolites for isotopic analysis. Freeze-dried urine samples were reconstituted with 3.6 ml of distilled water in cryovials and frozen.

Feces were used to estimate diet composition and diversity. We dried fecal samples to a constant mass in a forced-air oven at 50°C. A composite sample of feces was created for each site to estimate the proportion of plants within each forage group in the diets of muskoxen [i.e., graminoids (sedges and grasses), deciduous shrubs, lichens, mosses, evergreen shrubs, and forbs (including *Equisetum* spp.; Larter and Nagy 1997, 2004)]. Composite samples were created by selecting 5-10 pellets from each fecal sample collected at a site (Table 3.1). Microhistological analyses (150 views; Washington State University, Pullman, WA) were performed on the composite samples

to estimate major forage plants >5% in diet. The apparent dry matter digestibilities of forage groups for muskoxen (Ihl and Klein 2001, Ihl and Barboza 2007) were used to correct the relative densities of plant fragments for the differential digestion of forages (Leslie et al. 1983). We used the Shannon-Wiener Index (H') to estimate the diversity of the diet for each site (Krebs 1989).

Isotopic model of protein status

Isotope ratio mass spectrometry (IRMS) was used to measure the ratio of $^{15}N/^{14}N$ in excreta samples against atmospheric N (δ in ‰; Gannes et al. 1997) at the Forest Soils Laboratory at the University of Alaska Fairbanks (Fairbanks, AK) and the Marine Biological Laboratory (Woods Hole, MA). The accuracy of these systems was within 0.39‰ for $\delta^{15}N$ of peptone from meat. We used the following relationship to estimate the proportion of urea N derived from body N (*p*-UN; Barboza and Parker 2006) with samples of urine and feces from wild muskoxen:

$$p\text{-UN} = \frac{(\delta^{15}N_{Urea} + \Delta_{Urea} - \delta^{15}N_{Diet})}{(\delta^{15}N_{Body} - \delta^{15}N_{Diet})}.$$

We used steam distillation (Nolan and Leng 1972, Barboza et al. 1997) to collect urinary urea N from urine samples to measure the isotopic ratio of N in urea ($\delta^{15}N_{Urea}$). The discrimination factor Δ_{Urea} (2.90 ± 0.78‰, $\bar{x}$ ± SD) was determined from muskoxen in captivity that were in positive N balance (n = 6; Gustine et al. 2010). The $\delta^{15}N$ of the diet ($\delta^{15}N_{Diet}$) was estimated from $\delta^{15}N$ of residues of plant fibers in feces ($\delta^{15}N_{Fiber}$; Gustine et al., *in press*). A discrimination factor between diet and fecal fiber was derived from captive muskoxen fed grass hay (*Bromus spp.*; Δ_{Fiber} = 2.82 ± 0.50‰, n = 14; D. Gustine and P. Barboza, unpublished data).

The isotopic ratio of N in body tissue ($\delta^{15}N_{Body}$) was determined from the relationship between red blood cells and urinary creatinine ($\delta^{15}N_{Creatinine}$), which was isolated by high performance liquid chromatography (Xue et al. 1988, Barboza and Parker 2006). Studies of captive muskoxen, caribou, and reindeer were used to derive the following linear equation:

$$\delta^{15}N_{Body} = (\text{slope} \times \delta^{15}N_{Creatinine}) + \text{intercept}$$

where slope = 0.57 ± 0.42 and intercept = 5.64 ± 0.32 (standard error of estimate = 0.73; $n = 40$, $r^2 = 0.67$; **APPENDIX B**: Fig. B.1).

A spreadsheet-based simulation model (**APPENDIX C**: Fig. C.1) was developed to quantify the uncertainty in estimates of protein status for individual urine samples given the estimated endpoints of the linear model (i.e., $\delta^{15}N_{Diet}$ and $\delta^{15}N_{Body}$), the observed values of $\delta^{15}N_{Urea}$, and the variation in discrimination factors (Δ_{Urea} and Δ_{Fiber}). Each run of the model selected a random sample (with replacement) from distributions based on the parameters and their variation; stored the estimated *p*-UN for each run; and repeated the run 10,000 times. For the error associated with estimating each $\delta^{15}N$ via IRMS, we assumed that the error was drawn from a uniform distribution that was bounded by the measured $\delta^{15}N \pm 0.39‰$ (i.e., the accuracy of measuring the peptone standard). The Δ_{Urea}, Δ_{Fiber}, and the parameters used to estimate $\delta^{15}N_{Body}$ were sampled from a uniform triangular distribution that was bounded by the 95% confidence interval (Firko and Podleckis 2002). We used the means and standard deviations of $\delta^{15}N_{Fiber}$ for each sample site and the Box-Mueller scheme (Hilborn and Mangel 1997) to generate a different estimate of $\delta^{15}N_{Fiber}$ by sample site, and therefore $\delta^{15}N_{Diet}$, for each run of the model.

We used the median *p*-UN value from the 10,000 runs of the simulation model to estimate *p*-UN for each urine sample. We expected that samples low in absolute or percent N may produce measures of $\delta^{15}N$ that were highly variable. Therefore, we excluded samples with <1.4 micromoles of N in either urinary urea or creatinine. We also used the simulation model to exclude samples with unstable estimates. Unstable estimates were defined as urine samples with simulated ranges of *p*-UN that did not include 0 or 1 (e.g., range = 1.01 to 1.90) or absolute ranges of simulated values that were ≥1 (e.g., range = -1.25 to 1.25).

Characteristics of sample sites

We used spatial data with a GIS to estimate the elevation, slope, ruggedness of terrain, and large-scale vegetative associations at each site. Elevation (m) was estimated

from the U.S. Geological Survey's 60-m digital elevation model (DEM; U.S. Geological Survey 1999). Slope (°) was derived from the DEM in a GIS. We estimated a vector-ruggedness measure at the fine (0.18 km) and coarse (1.00 km) scale (Sappington et al. 2007). The Circumpolar Arctic Vegetation Map was used to identify the dominant vegetative associations at each site (Walker et al. 2002).

Statistics and data treatment

Descriptive statistics were used to report group sizes, physiographic characteristics, and diet composition and diversity among populations, while multiple regression was used to examine protein status of each group of muskoxen (i.e., mean *p*-UN by site) in relation to the population, year, and physiographic and dietary characteristics of each group (Zar 1999). The model set ($n = 11$) included the null model, population, year, and models derived from previous studies that implicated various characteristics of wintering sites that affect muskoxen (Table 3.2). Only sites with data for all variables were included in analysis. We used tolerance scores (<0.40) to evaluate multi-collinearity among the set of independent variables (Menard 2002). To minimize the number of variables in a model, we used principal component scores from the first and second axes to create variables for primary (first axis) and secondary (second axis) characteristics of both diet and terrain (Gotelli and Ellison 2004). Primary (PC1 diet) and secondary (PC2 diet) characteristics of diet comprised the proportion of each forage group in the diet and diet diversity. We derived primary (PC1 terrain) and secondary (PC2 terrain) terrain characteristics from elevation, slope, and vector ruggedness (0.18 and 1.00 km). A deviation contrast was used to code the categorical variables (i.e., population and year; Menard 2002). Akaike's information criterion adjusted for small sample sizes (AIC_c) and weights (w_i; Burnham and Anderson 2002) were used to evaluate the set of models; the w_i was interpreted as evidence (or support) for a model(s). We used coefficients (β), robust estimates of variance (Huber and Ronchetti 2009), and 95% confidence intervals to evaluate parameters in the models with the most support. We plotted observed values versus values of *p*-UN to qualitatively evaluate the dispersion of

model predictions by population.

A Shapiro-Francia's test (Zar 1999) was used to evaluate the assumption of normality for all comparisons. Stata 9.2™ (StataCorp, College Station, TX) was used for all statistical analysis.

Results

We collected 345 samples of urine and 306 samples of feces from 40 sites (**APPENDIX D**: Table D.1) in the wintering ranges of the 3 northern Alaskan populations (Fig. 3.1). Eighty-four urine samples were either too low in N to be measured precisely by IRMS (n = 40) or produced simulated ranges of p-UN values that violated the criteria for inclusion in our analyses (NS 2008 = 3; SP 2005 = 6; SP 2006 = 22; and SP 2008 = 13); therefore, we estimated protein status (p-UN) from 261 samples of urine (Table 3.1). The amounts of feces collected from 7 sites in 2005 was not sufficient for measures of $\delta^{15}N_{Fiber}$ and diet composition or diversity, so we described the diet composition and diversity for 33 sites or groups of muskoxen. Thus, we had estimates of diet and terrain characteristics and protein status for 30 sites (Table 3.1).

Groups of muskoxen consumed a variety of forages (Table 3.3; **APPENDIX D**: Tables D.2-D.4) at physiographically diverse sites (Table 3.1) across populations and years. Sampled groups from the NS and CT populations consumed diets that were primarily graminoids (25-73%, range), deciduous shrubs (3-48%), and mosses (3-37%). The dominant forages in the diets of groups of muskoxen in the SP population were lichens (5-54%), mosses (5-50%), and graminoids (3-48%; Table 3.3). The PC1 diet (variance explained = 36%) was correlated with lichens (r = 0.84), graminoids (r = -0.93), and diet diversity (r = 0.66); PC2 diet (variance explained = 26%) was correlated with mosses (r = -0.86) and deciduous shrubs (r = 0.73). Regarding elements of terrain, the PC1 terrain (variance explained = 63%) was correlated with both scales of vector ruggedness (r < -0.81); PC2 terrain (variance explained = 16%) was correlated with slope (r = -0.68).

The $\delta^{15}N$ of residues of plant fibers in fecal samples ($\delta^{15}N_{Fiber}$) was a marginal

predictor of major forages in the diets of muskoxen in late winter. The $\delta^{15}N_{Fiber}$ increased with the proportion of graminoids in the diet (0.11 ± 0.06, β ± 95% CI; Fig. 3.2). Conversely, the proportion of lichens increased in the diet as $\delta^{15}N_{Fiber}$ decreased (-0.07 ± 0.05; $r^2 = 0.203$); there was no relationship between $\delta^{15}N_{Fiber}$ and the amount of either mosses (-0.01 ± 0.04) or deciduous shrubs (-0.01 ± 0.03) in the diet.

The range of values for each component of the isotopic model of protein status (i.e., $\delta^{15}N_{Body}$, $\delta^{15}N_{Diet}$, and $\delta^{15}N_{Urea}$) exceeded 6‰ among populations and years (Fig. 3.3a; **APPENDIX D:** Tables D.5 and D.6). Indeed, the estimates of $\delta^{15}N_{Body}$, as derived from urinary creatinine, ranged from 1.43 to 8.54‰ ($n = 261$, 4.74 ± 1.03‰, $\bar{x}$ ± SD) for all the urine samples. The $\delta^{15}N_{Diet}$ was more depleted in ^{15}N (-2.64 ± 1.17‰; $n = 306$) with a smaller range in values than $\delta^{15}N_{Body}$ (-4.91 to 1.38‰). The largest range in $\delta^{15}N$ we measured was that of urinary urea N (-8.08 to 3.48‰) with a mean value that was typically depleted in ^{15}N (-2.20 ± 1.96‰; $n = 261$).

The protein status (*p*-UN) of muskox groups was highly variable across populations and years (Fig. 3.3b) but was correlated with characteristics of wintering sites. The model that corresponded to the abundance of preferred forages in late winter was the simplest explanation of protein status in muskoxen across populations and years (Table 3.2). This model explained 45% of the observed variance in protein status and performed adequately in estimating protein status in all 3 populations (1.00 ± 0.44, β ± 95% CI; 0.00 ± 0.22, intercept ± 95% CI; Fig. 3.4). The directions of the effects were as expected (Schaefer and Messier 1995a): the protein status of muskoxen improved (i.e., *p*-UN decreased) as the proportion of graminoids in the diet increased and elevation decreased [graminoids × -0.425 (± 0.31, 95% CI) + elevation × 0.766 (± 0.59) + 0.448 (± 0.22)].

Discussion

We identified a nutritionally-mediated mechanism that may explain some of the spatial variation in productivity in muskoxen populations. A non-invasive isotopically derived metric of protein status (*p*-UN) was linked to characteristics of wintering habitats

for muskoxen. Sedentary behavior by muskoxen during winter allowed us to link protein status and local foraging conditions. Declining forage availability in late winter increased the catabolism of body protein for body maintenance. Consequently, body stores of protein may limit pregnancy and lactation in these groups (White et al. 1989, White et al. 1997, Gustine et al. 2010). High variation in localized foraging conditions (Ihl 2010) may be strongly related to spatial heterogeneity in abiotic factors that created a diversity of foraging conditions in late winter that may eventually affect productivity of a population (e.g., SP; Gorn and Persons 2007).

Diet composition

As Ihl and Klein (2001) observed, lichens occurred in the diets of muskoxen in northern Alaska, but appeared more frequently in groups from SP. Unlike mosses (Ihl and Barboza 2007), the value of lichens as a winter food for muskoxen is unclear. To our knowledge, the reconstructed diets of the SP population contained the highest amount of lichens recorded for any muskox population. Lichens comprised approximately 23% of the diets in 4 years of sampling (Table 3.2). Use of lichens by muskoxen has been previously documented (e.g., Palmer 1944, McKendrick 1981), and even described as a "primary source of food" (Llano 1956). Indeed, Palmer (1944) reported small mass gains (3.5 kg) by 10-month old muskoxen eating lichens (*Cladonia* and *Cetraria* spp.) over a 10-day period. More recently, however, lichens have been considered unimportant forage for muskoxen (Klein 1992). Wild muskoxen tend to avoid lichens when other forages are available (Wilson 1992), but do consume lichens in late winter (Thing et al. 1987, Ihl and Klein 2001, Larter and Nagy 2004). Lichens are moderately digestible by muskoxen (47%; Ihl and Klein 2001), low in protein, and high in digestible carbohydrates (Storeheier et al. 2002a) but some species contain secondary metabolites that could incur handling costs for wintering muskoxen (e.g., usnic acid; Dailey et al. 2008, Sundset et al. 2008). As in caribou, lichens may provide a highly fermentable substrate that maintains favorable conditions for ruminal flora and fauna (Storeheier et al. 2002b) and may facilitate recycling of urea (Ørskov 1992). Based on the continued

occurrence of lichens in the diets of muskoxen on the SP (this study; Ihl and Klein 2001) and the potential impacts of a changing climate on the persistence of lichens in arctic and sub-arctic regions (Joly et al. 2009), the role and value of lichens as winter forage for muskoxen needs to be clarified.

Protein status

For muskoxen in late winter, protein status (*p*-UN) is a relative and robust index of the dynamics of body protein that is most sensitive to changes in $\delta^{15}N_{Urea}$. In reindeer, when *p*-UN > 0.46, animals are assumed to be in negative nitrogen balance due to demands for either nitrogen or energy (Barboza and Parker 2006). Unfortunately, this relationship has not been established for muskoxen but we have no reason to suspect that the relationship would be dissimilar. The $\delta^{15}N_{Urea}$ is robust to daily feeding patterns in muskoxen that could affect dietary and endogenous inputs into the circulating pool of urea N (P. Barboza, unpublished data). As noted in other ruminants (Van Soest 1994), the size of the body urea pool is relatively stable in muskoxen even though the rate of urea formation increases with food intake between spring and autumn (P. Barboza, unpublished data). Thus, changes in $\delta^{15}N$ of urea reflect shifts in the source of N between body and diet rather than contraction or expansion of the urea pool. Indeed, estimates of *p*-UN are driven primarily by changes in $\delta^{15}N_{Urea}$ ($r = 0.88$). The variance and range of values for $\delta^{15}N_{Urea}$ were larger than either the $\delta^{15}N_{Diet}$ or $\delta^{15}N_{Body}$ (Fig. 3.3a) and were responsible for the high variance in *p*-UN among groups of muskoxen within these 3 populations (Fig. 3.3b).

Our model set to evaluate the prevailing literature on foraging constraints on protein status was conclusive: there was strong support ($w_i = 0.90$) for the model that most closely aligned with forage abundance in late winter. Surprisingly, of all the candidate models, the one with the least support was the amount of mosses in the diet (Table 3.2). Due to the apparently poor value of mosses as forage (Ihl and Barboza 2007), the low performance of this model merits some clarification. As in those previous works, we reanalyzed the relationship between protein status and the proportion of moss

fragments in feces without correcting for digestibility, but the model was not improved ($w_i = 0.001$, $r^2 = 0.01$). Moss in the reconstructed diets of muskoxen may only be valuable as an index of foraging conditions if an increase in occurrence of moss in the diet corresponds with a decrease in the amount of preferred forages. For example, the amount of graminoids in the diets were more negatively correlated with lichens (r = -0.74) than mosses (r = -0.21). Additionally, the higher fragmentation of mosses during digestion may overestimate occurrence of mosses in the feces (Dearden et al. 1975) and muskoxen may not be able to avoid consumption of some moss because preferred forages often grow among the moss pads (Ihl 2007). Therefore, the more direct index of foraging conditions may be to monitor shifts in the amount of graminoids in the diet.

The availability of preferred forage in late winter (Table 3.2) explained a large portion of the observed variance (45%) in protein status among groups of muskoxen across populations and years (Fig. 3.4). Groups of muskoxen that resided at higher elevations and consumed fewer graminoids relied more heavily on body proteins in late winter. The elevation term was likely related to both vegetative productivity and snow conditions that affected availability of forage. Elevational gradients in moisture strongly influence the productivity of vegetation in arctic systems. Mesic sites at lower elevations are typically more productive than sites on exposed ridges where muskoxen congregate in winter (e.g., Williams and Rastetter 1999). In winter, prevailing winds and topographic diversity affect the deposition and condition of snow as well as the vegetative communities that persist on wind-scoured ridges (Bliss 1962). In winter, muskoxen consistently select for wetter foraging sites at lower elevations where graminoid biomass is high (Schaefer and Messier 1995a). Graminoids are typically higher in crude protein (4-9%; Larter and Nagy 2001c) than other winter foods such as mosses and lichens (3-6%; Boertje 1981), and are principal components of the winter diet of muskoxen in Alaska (this study, Ihl and Klein 2001, Reynolds et al. 2002), Greenland (Thing et al. 1987), Canada (Parker 1978, Larter and Nagy 2004), and Russia (Rapota 1984). Our modeling effort supports these observations, as the amount of graminoids in the diet was negatively correlated with p-UN. For muskoxen in more mountainous environments,

snow accumulation at lower elevations and on leeward slopes effectively "forced" groups of muskoxen to move to wind-swept areas at higher elevations (Thing 1984). As winter progressed and the energetic costs of moving to other foraging locations became prohibitive (Charnov 1976), these groups became restricted to smaller, less productive sites (i.e., less graminoids) for the duration of the winter (Schaefer and Messier 1995b). Indeed, Klein (1992) noted that mountain habitats likely offered lower carrying capacities than steppe environments because muskoxen have little ability to adapt to snow-rich environments.

Winter conditions could limit the productivity of muskox populations (Forchhammer and Boertmann 1993, Reynolds 1998, Moen et al. 2006). Severe winters reduce forage availability, increase costs of foraging (Parker 1978, Thing et al. 1987), shorten the growing season, and, subsequently, reduce the period of mass gain (Reynolds et al. 2002) and thus the amount of body protein available for reproduction (Gustine et al. 2010). Winter conditions and the associated impacts to population dynamics, however, can be highly variable in space and time. Spatial heterogeneity in abiotic factors (e.g., snow depth and condition) can dampen effects of density dependence, while temporal variation in winter conditions (e.g., rain on snow events) increases the strength of density-dependent feedbacks on population productivity (e.g., Coulson et al. 2001, Wang et al. 2006). Physiographic diversity (Nellemann 1998) creates spatially diverse snow and foraging conditions that may benefit (i.e., better protein status) some groups by increasing access to forage in late winter (Fig. 3.4). Clearly, there are gradients of physiographic diversity that can create both favorable and unfavorable foraging conditions. Mountainous environments offer diverse foraging conditions at large spatial scales but high variability in snow deposition essentially "strand" muskoxen on small islands of winter habitat. Conversely, wind-swept coastal environments with low physiographic diversity at coarse scales have typically less snow accumulation as well as micro-topographic conditions that create favorable foraging conditions throughout the winter for muskoxen. However, when winters are severe (e.g., rain on snow events early in winter, excessive snowfall) or prolonged, persistently poor foraging conditions may

overwhelm beneficial effects of physiographic diversity at any scale: the protein status of muskoxen groups would deteriorate and the variance in protein status among groups would decline as the spatial variance in resource availability declines (Post and Forchhammer 2004). The effects of severe winters should be amplified for muskoxen confined to small wintering areas and at higher densities (e.g., muskoxen in mountainous environs; Larter and Nagy 2001b). We documented one such severe event, where muskoxen in the SP were challenged by the record-setting winter of 2008 (total snowfall by mid-April = 268 cm; National Climatic Data Center 2008): almost all of the muskoxen we sampled were in moderate to poor protein status (p-UN > 0.40; Fig. 3.3b) with the least amount of graminoids in the diets of all populations and years (3-22%, range; Table 3.3). Therefore, as monitoring efforts intensify, mean values of protein status or other metrics of body condition in late winter may be more valuable if interpreted in the context of the variance of protein status over spatio-temporal scales.

Mechanisms behind the changes in population trajectories are often elusive in ecology (McNamara and Houston 2008) with significant impacts to both the conservation and management of large herbivores (Gaston et al. 2009). We applied an isotopic approach that estimated endogenous and exogenous contributions to N in the urinary urea of wild muskoxen. Although, population- and year-level comparisons were inconclusive, the variance in physiography and foraging conditions at smaller scales affected access to more productive foraging sites and this corresponded with protein status for groups of muskoxen. Given this apparent susceptibility of muskoxen groups to localized foraging conditions, there is a clear need to account for climate-weather-topography effects at multiple spatial and temporal scales when predicting the potential impacts of climatic shifts on population trajectories of muskoxen and other ungulates (Loe et al. 2005, Pettorelli et al. 2005). Certainly, other factors such as the densities of muskoxen in suitable wintering habitat (Larter and Nagy 2001a), age, sex, and reproductive status (Adamczewski et al. 1997, Peltier and Barboza 2003) should also explain a large portion of the remaining variance in protein status. Discerning relationships among these factors and protein status will certainly provide important insights into behavioral, physiological,

and ecological mechanisms in the population dynamics of muskoxen. However, this isotopically-derived estimate of protein status identified a potentially important mechanistic link between highly localized foraging conditions and the spatial variation in productivity of a very sedentary herbivore. This novel use of N isotopes could also be used to monitor protein status in populations of other northern ungulates, such as bison (*Bison bison*) and mountain sheep (*Ovis* spp.). With further refinement and development (e.g., technique to estimate sex and reproductive status in urine-in-snow samples), isotopic monitoring may become an important tool to elucidate important factors in the nutritional ecology of northern ungulates.

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Table 3.1. Number of sites and excreta samples collected and those included in analyses (in parentheses) for protein status as well as physiographic characteristics of wintering sites of groups of muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in Alaska, April, 2005-2008.

Population	Year	Sites	Samples		Group size	Elevation (m)	Slope (°)	Vector-ruggedness (180 m)[a]	Vector-ruggedness (1 km)[a]	Vegetation (%)[b]
			Urines	Fecals	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	
NS	2007	3 (3)	30 (28)	30	44 ± 1.5	179 ± 170	1 ± 1.2	0.7 ± 0.72	6.7 ± 6.31	Erect shrub tundra (33%) and wetlands (67%)
	2008	3 (3)	30 (25)	30	43 ± 2.9	53 ± 42	1 ± 0.3	0.0 ± 0.02	47.2 ± 46.74	
CT	2007	3 (3)	30 (27)	30	25 ± 3.5	149 ± 27	22 ± 8.7	1.1 ± 0.59	52.1 ± 17.42	Graminoid tundras (100%)
SP	2005	12 (4)	48 (30)	20	20 ± 3.6	242 ± 41	17 ± 4.5	18.8 ± 8.38	78.4 ± 22.31	Barrens (16%), erect shrub tundra (64%), graminoid tundras (16%), and wetlands (4%)
	2006	8 (7)	97 (65)	86	24 ± 3.4	286 ± 58	10 ± 1.3	5.5 ± 3.61	40.3 ± 9.86	
	2007	5 (5)	50 (47)	50	20 ± 0.3	212 ± 103	26 ± 9.6	32.5 ± 27.23	93.3 ± 45.87	
	2008	6 (5)	60 (39)	60	23 ± 2.7	299 ± 21	28 ± 6.9	13.4 ± 4.61	133.5 ± 28.21	

[a]Sappington et al. (2007) estimate of vector ruggedness × 10^3

[b]Walker et al. (2002)

Table 3.2. Models used to evaluate the observed variance in protein status for groups of muskoxen (n = 30) in 3 populations from Alaska, April, 2005-2008.

Rationale for model structure	Model	K[a]	w_i[b]	r^2 or R^2[c]
Abundance of preferred forages in mesic environments at lower elevations (Schaefer and Messier 1995a).	Graminoids[d] + elevation	3	0.895	0.448
Amount of preferred forages in the diet (Klein 1992, Ihl and Klein 2001, Larter and Nagy 2001a).	Graminoids	2	0.027	0.241
Terrain characteristics (Nellemann 1998) and the amount of preferred forages in the diet (Klein 1992, Ihl and Klein 2001, Larter and Nagy 2001a)	PC1 terrain[e] + graminoids	3	0.025	0.298
Terrain (Nellemann 1998) and diet characteristics (Larter and Nagy 2001a, Gunn and Adamczewski 2003).	PC1 terrain + PC1 diet[f]	3	0.018	0.282
Terrain-ruggedness index as proxy for snow conditions (Nellemann and Reynolds 1997)	Vector-ruggedness measure[g]	2	0.012	0.200
Effects due to inter-annual variance in environmental conditions (Gunn and Adamczewski 2003, Moen et al. 2006).	Year	4	0.007	0.300
Proxy for sources of variation due to effects of population.	Population	3	0.006	0.227
Influence of terrain characteristics on snow conditions (Nellemann 1997, 1998)	PC1 terrain + PC2 terrain[e]	3	0.004	0.201
Null	Intercept only	1	0.001	n/a
As more preferable forages becomes less available, muskoxen expand dietary breadth to include less preferred forages and may rely more heavily on body stores (Larter and Nagy 2004; Ihl 2010)	Diet diversity (H')	2	0.001	0.064
Mosses as indicator of range conditions (Ihl and Barboza 2007; Ihl 2010).	Mosses[d]	2	0.001	0.011

[a]Number of parameters.

[b]Akaike weights.

[c]Coefficients of determination for simple linear (r^2) or multiple (R^2) regression.

[d]Proportion of item in the diets as estimated from microhistology corrected for differential digestion of forages.

[e]Scores from first (PC1 terrain) or second (PC2 terrain) principal component that includes elevation (km), slope (°), and vector ruggedness at the fine (180 m) and coarse scale (1,000 m; Sappington et al. 2007).

[f]Scores from first principal component that includes diet composition by functional group and diet diversity.

[g]Estimate of the vector ruggedness measure at 1-km resolution (Sappington et al. 2007).

Table 3.3. Diet composition and diversity diets ($\bar{x} \pm$ SE) for groups of muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in Alaska during April, 2005-2008.

Component of diet	NS		CT	SP			
	2007	2008	2007	2005	2006	2007	2008
	($n = 3$)	($n = 3$)	($n = 3$)	($n = 5$)	($n = 8$)	($n = 5$)	($n = 6$)
Graminoids[a]	56.8 ± 9.5	43.1 ± 12.7	54.1 ± 9.4	26.2 ± 4.4	32.8 ± 4.3	17.7 ± 4.0	10.3 ± 2.8
Deciduous shrubs	6.7 ± 1.7	25.6 ± 12.1	15.1 ± 5.6	7.0 ± 1.1	5.3 ± 1.6	8.8 ± 1.6	12.4 ± 3.3
Lichens	2.7 ± 1.5	3.4 ± 2.4	3.7 ± 1.4	23.5 ± 7.8	28.2 ± 4.0	32.2 ± 8.1	39.1 ± 3.9
Mosses	23.9 ± 6.7	11.3 ± 4.1	15.1 ± 6.1	33.5 ± 5.6	27.9 ± 4.1	27.3 ± 3.8	21.4 ± 2.9
Evergreen shrubs	2.1 ± 0.6	5.8 ± 1.3	9.5 ± 3.3	7.8 ± 1.8	4.2 ± 1.0	9.0 ± 1.3	16.0 ± 3.7
Forbs[b]	7.8 ± 4.9	10.8 ± 7.0	2.5 ± 2.0	2.1 ± 0.9	1.7 ± 0.5	5.0 ± 3.7	0.7 ± 0.2
Diversity (H')[c]	1.57 ± 0.19	1.66 ± 0.20	1.59 ± 0.14	1.89 ± 0.04	1.84 ± 0.06	1.96 ± 0.06	1.80 ± 0.04

[a]Sedges and grasses.

[b]Includes *Equisetum* spp.

[c]Shannon-Wiener index of diversity (Krebs 1989).

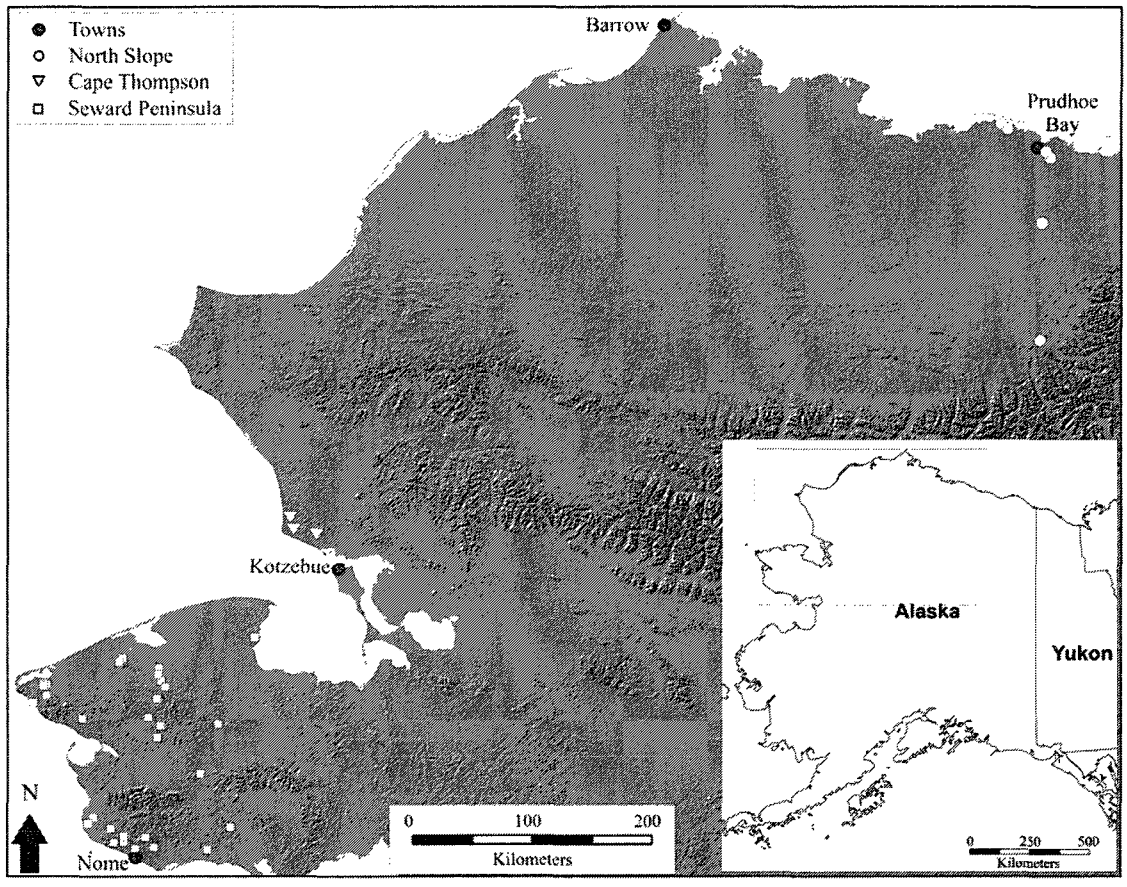

Figure 3.1. Groups of muskoxen (n = 40) in 3 populations on a hill-shaded relief image (as determined from a digital elevation model), April, 2005-2008.

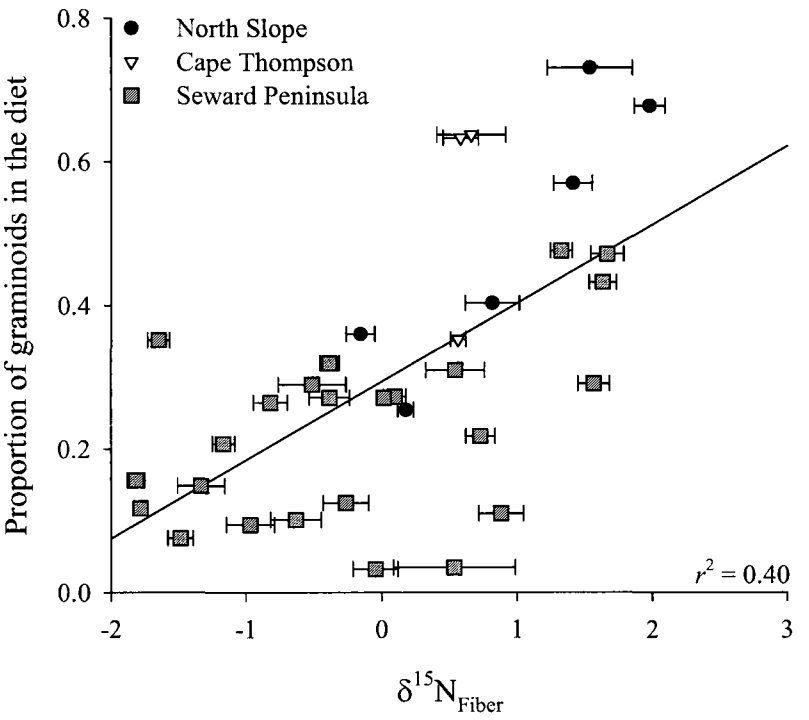

Figure 3.2. The relationship between the proportion of graminoids in the diet and $\delta^{15}N$ of residues of plant fiber in feces ($\delta^{15}N_{Fiber}$) collected from 3 populations of muskoxen in Alaska during April, 2005-2008.

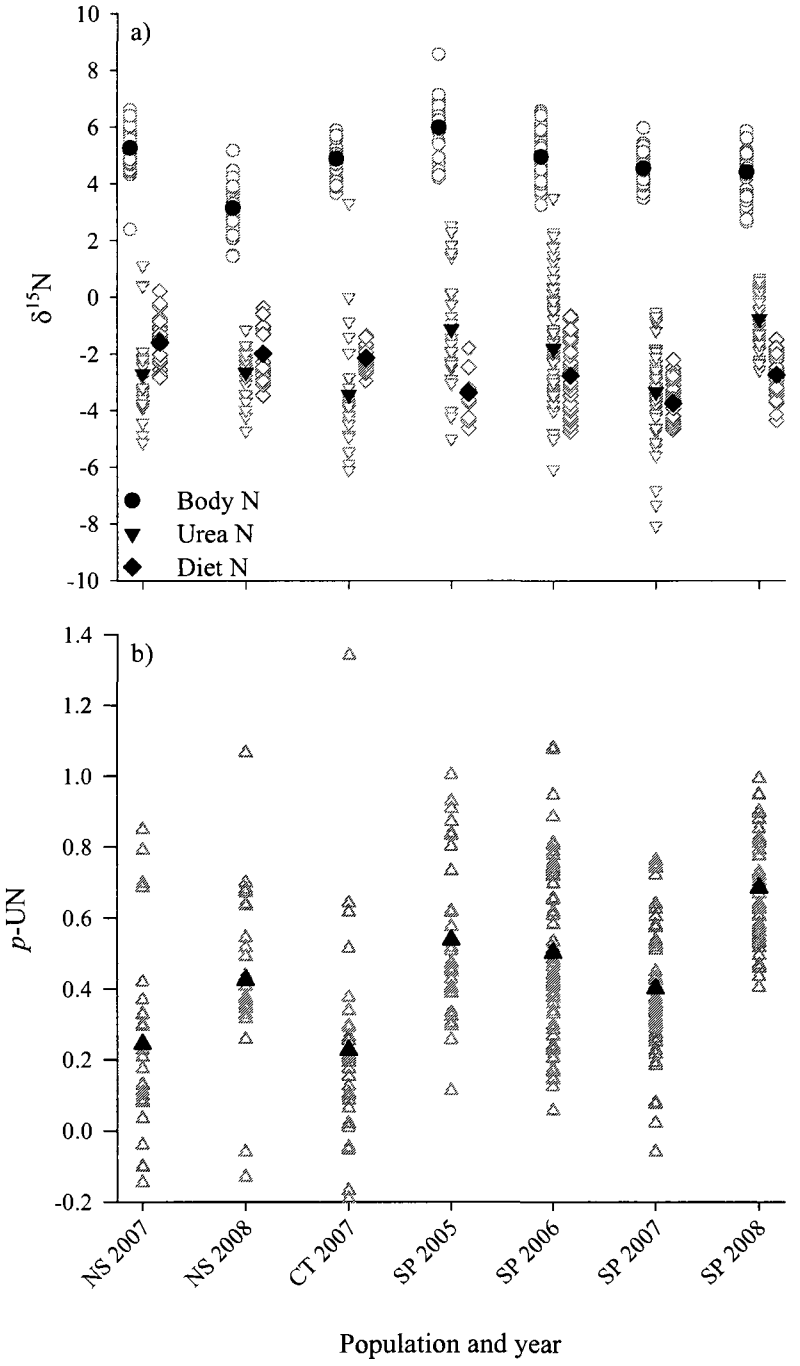

Figure 3.3. Means (black symbols) and distributions (light gray symbols) of a) ratios of $^{15}N/^{14}N$ (δ) in urinary urea, diet, and body N and b) the proportion of urea N derived from body N (*p*-UN) for 3 populations of muskoxen [the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP)] in Alaska during April, 2005-2008.

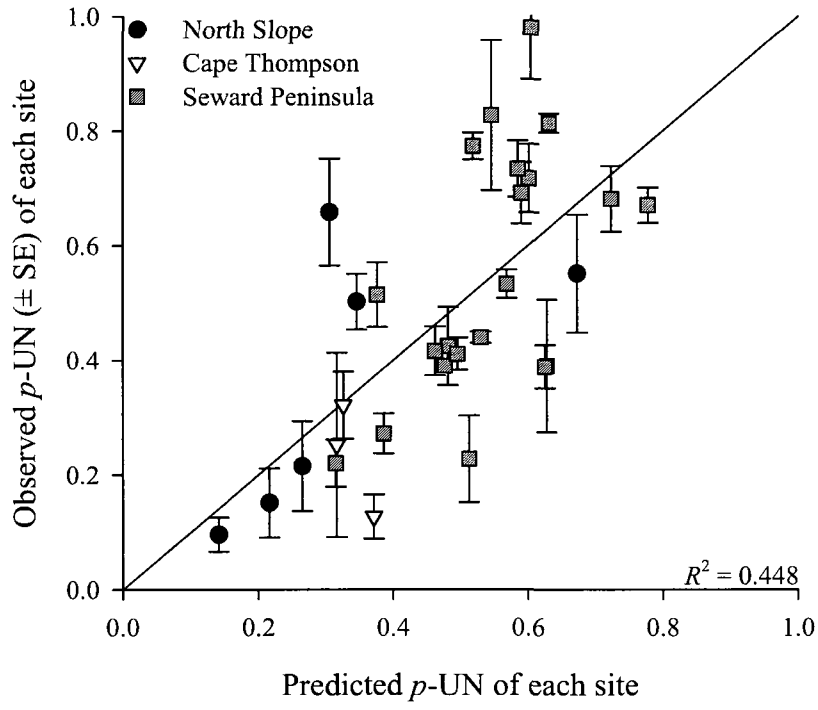

Figure 3.4. Observed estimates of the proportion of urea N derived from body N (*p*-UN) on the predicted values of *p*-UN [as estimated from the model that includes the proportion of graminoids in the diet, elevation (m), and the intercept] at sites used by 3 populations of muskoxen in Alaska, 2005-2008; the 1:1 slope is denoted by the solid line.

CHAPTER 4 - AN ISOTOPIC APPROACH TO MEASURING NITROGEN BALANCE IN CARIBOU[a]

Abstract

Nutritional restrictions in winter may reduce the availability of protein for reproduction and survival in northern ungulates. We refined a technique that uses recently voided excreta on snow to assess protein status in wild caribou (*Rangifer tarandus*) in late winter. This was the first application of this non-invasive, isotopic approach to assess the protein status of wild caribou by determining the dietary and endogenous contributions of N to urinary urea. We used isotopic ratios of N ($\delta^{15}N$) in urine and fecal samples to estimate the proportion of urea N derived from body N (*p*-UN) in pregnant, adult females of the Chisana Herd, a small population that ranges across the Alaska-Yukon border. We took advantage of a predator-exclosure project to examine the N status of penned caribou in April 2006. Lichens were the primary forage (>40%) consumed by caribou in the pen and $\delta^{15}N$ of fiber tracked the major forages in their diets. The $\delta^{15}N$ of urinary urea for females in the pen was depleted (-1.3 ± 1.0‰, $\bar{x}$ ± SD) relative to the $\delta^{15}N$ of body N (2.7 ± 0.7‰). A similar proportion of animals in the exclosure lost core body mass (excluding estimates of fetal and uterine tissues; 55%) and body protein (estimated by isotope ratios; 54%). This non-invasive, isotopic approach may prove valuable in examining inter- and intra-annual changes in protein stores of northern herbivores.

Introduction

Nitrogen (N) is a limiting nutrient for many herbivores because leaves and stems of plants have low concentrations of N required for the synthesis of body protein in the animal (White 1993). Nitrogen balance is synonymous with protein balance in animals: N is gained from the diet in positive balance as N is incorporated in body protein but lost from the body when dietary N intake is inadequate to maintain body protein during a negative balance. Northern ungulates rely on body stores to survive and reproduce

[a]Gustine, D. D., P. S. Barboza, L. G. Adams, R. G. Farnell, and K. L. Parker. 2010. An isotopic approach to measuring nitrogen balance in caribou. Journal of Wildlife Management: *in press*.

because plant growth is limited to summer. Females must support pregnancy and lactation through body stores until plant growth resumes in spring (DelGiudice et al. 1990, Adamczewski et al. 1997, Cook et al. 2004, Barboza and Parker 2008). Body fat is the primary energy store of ungulates (Price and White 1985) whereas body proteins are primarily used as a source of N for maintenance of critical tissues and production of a calf (Gerhart et al. 1996, Gustine et al. 2010). However, stores of body protein may be depleted quickly if proteins are used for energy when fat stores are exhausted (Barboza et al. 2009). Consequently, protein stores that are needed for reproduction may be depleted when food supplies are low and high energy demands are high during severe winters (Parker et al. 2009).

Nutritional restrictions during the last trimester of pregnancy can impair fetal growth and development (Rognmo et al. 1983, Sams et al. 1995), and consequently, females may produce small offspring (Reimers 1997, Festa-Bianchet and Jorgenson 1998, Adams 2005) with poor survivorship (Albon et al. 1987, Skogland 1990). Annual N demands peak during lactation for adult females but these demands generally cannot be met by intake alone and require the use of body stores (Chan-McLeod et al. 1994, Barboza and Parker 2008). Growth of offspring can be impaired by nutritional restriction of the mother during pregnancy and early lactation (Albon et al. 1987, Mech et al. 1987, Forchhammer et al. 2002, Adams 2003). Neonatal growth rates are directly correlated with the protein content of maternal milk (Robbins et al. 1981). Therefore, the ability of reproductive females to gain (McArt et al. 2009) and maintain maternal stores of N in body protein is crucial for the production, growth, and survival of offspring (Allaye-Chan 1991, Landete-Castillejos et al. 2001, Barboza and Parker 2008).

Monitoring changes in the stores of body protein of individuals is a valuable tool for assessing nutritional influences on population trends, but seasonal changes in body protein are difficult to measure because the changes may be small in comparison with the total mass of body protein (Torbit et al. 1985, Chan-McLeod et al. 1994, Gerhart et al. 1996). Most techniques to assess protein status are often impractical for large animals in the wild because they require repeated measures of body composition in the same animal

[e.g., ultrasound measurements of loin thickness (Cook et al. 2004); estimates of body water content (Parker et al. 1993)] or cross-sectional comparisons of body composition among large numbers of animals [e.g., seasonal harvests (Chan-McLeod et al. 1994, Gerhart et al. 1996)]. Concentrations of nitrogenous metabolites (urea and creatinine) in urine deposited in snow has been used as an index of the catabolism of body protein in ungulates (e.g., DelGiudice et al. 2001, Larter and Nagy 2001) but this measure may be confounded, in part, by changes in renal function of northern ungulates during winter (Säkkinen et al. 2001, Parker et al. 2005). Barboza and Parker (2006) presented a non-invasive, isotopic approach to index the catabolism of body proteins in captive reindeer (*Rangifer tarandus*): the proportion of urinary urea N that is derived from body N (*p*-UN; Fig. 4.1). This technique uses the isotopic ratio ($^{15}N/^{14}N$ relative to atmospheric N; $\delta^{15}N$) of N metabolites to assess the dietary and endogenous contributions of N to urinary urea. Because body protein has a higher $\delta^{15}N$ than dietary sources of protein (Kelly 2000), an increase in the catabolism of body protein results in an increase in the $\delta^{15}N$ of urinary urea and, consequently, an increase in *p*-UN. Values of *p*-UN > 0.46 indicate a negative N balance, whereas *p*-UN $\leq$ 0.46 indicates that animals are maintaining or gaining body protein (Barboza and Parker 2006). Until now, this isotopic approach had not been used to estimate the protein status of wild northern ungulates.

We took advantage of a unique opportunity to use this non-invasive isotopic technique where wild caribou were being temporarily held in late winter within a large paddock on native range. The Chisana Herd (CH), ranging across the Alaska-Yukon border is a small, declining herd (approx. 770 caribou) and is considered "at risk" in the Yukon (Farnell and Gardner 2002). During 2003-2006, the Yukon Department of the Environment, in collaboration with the U.S. National Park Service, U.S. Geological Survey, Canadian Wildlife Service, White River First Nation, and Alaska Department of Fish and Game, conducted a predator-exclosure experiment in an attempt to increase the survival of neonates (Chisana Caribou Recovery Team 2010). Pregnant caribou were captured in late winters of 2003 to 2006 and held in a temporary predator exclosure (pen; 6.0 to 12.2 ha) in the Kluane Wildlife Sanctuary in southwest Yukon. Females gave birth

in the pen and cow-calf pairs were released back into the wild population in mid-June when most calves were approximately 3-5 weeks old.

Our objective was to validate this isotopic technique by assessing diet and protein status in a semi-captive (penned) population of pregnant caribou and to identify the potential challenges of population-level assessments of protein status in wild caribou. We examined the use of residues in feces as an isotopic proxy of $\delta^{15}N$ for the diets of penned caribou that were eating natural forages and a formulated diet; and compared changes in core body tissues (excluding fetal and other reproductive tissues) with the isotopic method to estimate *p*-UN. We expected that the $\delta^{15}N$ of plant residues in the feces would correspond to the proportion of major forages in the diet; and that caribou in the exclosure would generally be in positive protein status as a result of supplemental feeding (i.e., gain core body tissues and $p\text{-UN} \leq 0.46$).

Study Area

Climate in the region was continental with average annual temperatures below freezing (-6°C) and most of the annual precipitation (~32 cm) fell as snow. Low elevations of the CH's range consisted of spruce (*Picea* spp.) woodlands dominated by white (*P. glauca*) and black (*P. mariana*) spruce (Farnell and Gardner 2002). Treeline occurred at about 1,200 m. Subalpine vegetation [willow (*Salix* spp.), dwarf birch, and blueberry (*Vaccinium vitas-idaea*) and sedge (*Carex* spp.) tussocks] graded into alpine areas that contained mosaics of talus, scree, sedge, mountain avens (*Dryas* spp.), heath (*Cassiope* spp.), graminoids, lichens, and mosses (Farnell and Gardner 2002, Lenart et al. 2002).

The pen was located within the herd's winter range at Boundary Lake, 80 km south of Beaver Creek, YT. Selection of the site was based on the following criteria: proximity to capture operations and regularly used summer ranges; reasonable aircraft access to support the pen operations; and a number of large trees to act as fence posts and as cover for animals while allowing visibility to monitor animals (Chisana Caribou Recovery Team 2010).

Methods

Caribou and reindeer are referenced throughout this work. Although caribou and reindeer are the same species (*Rangifer tarandus*), some behavioral, morphological, and physiological differences merit a distinction (Barboza and Parker 2008). We use reindeer in reference to the domesticated or semi-domesticated form of *Rangifer tarandus* in North America that were derived from Eurasian stocks; caribou as the wild North American representative of this species; and *Rangifer* sp. as the term for both reindeer and caribou.

Female caribou were captured with a net gun from a helicopter (Rongstad and McCabe 1984) and sedated with medetomidine (10 mg caribou^{-1}; 0.07-0.10 mg kg^{-1}) delivered intranasally (Cattet et al. 2004) to minimize stress during handling and helicopter transport to the exclosure. Animals were blindfolded, hobbled, and trussed in restraint bags for transport inside the helicopter to the pen. Pregnancy was determined by transrectal ultrasound (Ropstad et al. 1999); individuals that were not pregnant were released outside the exclosure. Each animal was weighed (±0.5 kg) on an electronic scale, and fitted with a VHF radiocollar with a uniquely numbered marking band for visual identification. The sedative was reversed with atipamezole (30 mg caribou^{-1}; 0.2-0.3 mg kg^{-1}). Procedures for capture and handling followed guidelines established by the American Society of Mammalogists (Gannon and Sikes 2007).

Penned caribou were provided with a complete pelleted ration, as described in Barboza and Parker (2006), and terrestrial fruticose lichens. Fruticose lichens were mainly *Cladina arbuscula, C. mitis,* and *C. stellaris* collected the previous autumn in the vicinity of Whitehorse, YT, Canada. Foods for animals in the exclosure were provided at 3.0 kg·animal^{-1}·d^{-1} for the ration and 0.5 kg·animal^{-1}·d^{-1} for lichens; caribou also consumed natural forages available in the exclosure. Water was available within the pen as snow throughout the study.

Body masses of individual caribou were measured opportunistically during feeding with 4 electronic platform scales positioned at 2 feeding stations. Females were observed regularly each day during calving. Calves were captured and weighed to the

nearest 0.1 kg on a spring scale within 24 h of birth. For calves that were not weighed on the day of birth ($n = 2$), we estimated birth mass from the proportional mass gains reported for caribou in the Denali herd (Adams 2005). One calf was consumed by a predator or scavenger before it could be weighed.

Isotopic model of N balance

We used isotope ratio mass spectrometry (IRMS) to measure enrichment of ^{15}N (δ in ‰) in food and excreta samples in reference to atmospheric N (Gannes et al. 1997). Isotopic analyses were conducted by the Alaska Stable Isotope Facility (University of Alaska Fairbanks, Fairbanks, AK; UAF), the Forest Soils Laboratory (UAF), and the Marine Biological Laboratory (Woods Hole, MA). The accuracy of these systems was within 0.39‰ for $\delta^{15}N$ of peptone from meat.

We used the following relationship to estimate *p*-UN (Fig. 4.1) from urine in snow (urine) and fecal samples (Barboza and Parker 2006):

$$p\text{-UN} = \frac{(\delta^{15}N_{Urea} + \Delta_{Urea} - \delta^{15}N_{Diet})}{(\delta^{15}N_{Body} - \delta^{15}N_{Diet})}.$$

Urea N was isolated from samples of urine to measure $\delta^{15}N_{Urea}$. We used a discrimination factor (Δ_{Urea}) determined for *Rangifer* sp. in captivity that were in positive N balance (Parker et al. 2005; Barboza and Parker 2006, 2008). The $\delta^{15}N_{Diet}$ was determined from residues of plant fibers in fecal samples (D. Gustine, P. Barboza, and J. Addison, unpublished data). After isolating urinary creatinine to measure $\delta^{15}N_{Creatinine}$, we estimated the $\delta^{15}N_{Body}$ from a linear relationship between $\delta^{15}N$ of red blood cells or muscle and $\delta^{15}N_{Creatinine}$ in captive and wild *Rangifer* sp. (**APPENDIX B**: Fig. B.1).

Collection and processing of samples

Food — We collected 2 samples of approximately 50 g of the ration during each week in captivity (9, 16, 23, and 30 April). Representative (50-100 g) samples of lichens were collected from bags prior to shipment to the exclosure in 2006. Ration and lichen samples were dried in a forced-air oven at 50°C to constant mass (>96 h) and then ground through a 1-mm screen in a Wiley mill (Arthur Thompson Company, Philadelphia, PA).

Foods were assayed for total N, neutral and acid detergent fiber, lignin, and ash content (Table 4.1; Barboza and Parker 2006).

Excreta — We sampled excreta from penned caribou from 9-30 April 2006. Samples of urine were collected 4 weeks after the animals were captured. We collected urine in snow (urine) opportunistically over a 2-day period (25-26 April; $n = 30$) by selecting discrete samples that were recently voided; due to low N, 4 samples were excluded from analysis. We did not attempt to collect samples from individual animals; therefore, estimates of N balance represent the population of caribou in the exclosure.

We collected urine (approx. 100 ml) and feces (approx. 25 g) into plastic bottles and bags with leak-proof seals (VWR International, West Chester, PA). We used a small trowel to assist in collecting the most concentrated portion of each urine sample; the trowel was thoroughly cleaned after each collection. To concentrate the urinary metabolites (urea and creatinine) for isotopic analysis, we lyophilized and reconstituted the urine samples with 3.6 ml of distilled water in cryovials (Nalge Nunc International) and stored the concentrate at -20°C. We collected urinary urea from urine samples by steam distillation (Nolan and Leng 1972, Barboza et al. 1997). Urinary creatinine was isolated by high performance liquid chromatography (Xue et al. 1988, Barboza and Parker 2006).

We collected 5 composite fecal samples each week (9, 16, 23, and 30 April) to monitor diet composition and the $\delta^{15}N$ of the diet. Each composite sample consisted of 5 pellets from each of the 5 pellet groups. All samples were placed in plastic bags and kept frozen until processing. Fecal samples were dried to a constant mass at 50°C in a forced-air oven. The Wildlife Habitat Nutrition Laboratory at Washington State University, Pullman, WA performed microhistological analyses to forage class and major forage plants >5% in diet (level B) at 100 views. We used the apparent dry matter digestibility of major forage groups from caribou on a similar diet (Table 4.2) to correct the relative density of plant fragments for digestion of forages (Leslie et al. 1983).

We used residues of plant fibers from composited fecal samples (fiber) to estimate $\delta^{15}N_{Diet}$. Dried fecal samples were ground in a Wiley mill through a 1-mm screen for

analysis. Fecal samples were extracted in sealed filter bags (ANKOM Technology, Macedon, NY) that were previously washed with petroleum ether and air-dried to remove any N associated with residues on the polyester. Approximately 2 g of fecal material from each sample was divided into 2 filter bags. Fecal samples were rinsed with distilled boiling water to remove N from endogenous secretions (Van Soest 1994). We rinsed the bags individually (approx. 1.0-1.3 L in 4-5 rinses at 20 min·rinse^{-1}), dried them overnight at 50°C, and analyzed the residues by IRMS.

Calculations and statistical analyses

Deriving $\delta^{15}N$ of the diet — We measured the $\delta^{15}N_{Fiber}$ in duplicate for each composite fecal sample. We determined that the $\delta^{15}N_{Fiber}$ of captive *Rangifer* sp. was enriched by 3.34 ± 1.17‰ (Δ_{Fiber}; $\bar{x}$ ± SD; n = 26; D. Gustine, P. Barboza, and J. Addison, unpublished data) above the $\delta^{15}N$ of mixed and 100% lichen diets (Fig 4.1). Therefore, we used Δ_{Fiber} and the $\delta^{15}N_{Fiber}$ to estimate $\delta^{15}N_{Diet}$. For inputs to the isotopic model of protein status, we used the average $\delta^{15}N_{Fiber}$ of the fecal samples collected on 23 and 30 April.

Estimating $\delta^{15}N$ of urinary urea and body N — The $\delta^{15}N_{Urea}$ in the isotopic model was corrected for changes in $\delta^{15}N$ that occurred when urea was formed from dietary sources of N (Δ_{Urea}; Fig 4.1). From previous research on captive *Rangifer* sp. (Parker et al. 2005; Barboza and Parker 2006, 2008), we estimated Δ_{Urea} for animals that were in positive N balance on formulated diets (n = 15; $\delta^{15}N$ of the diet - $\delta^{15}N$ of urinary urea = 2.35 ± 0.89‰). Regarding the $\delta^{15}N_{Body}$, we used a linear regression (standard error of estimate = 0.73; n = 40, r^2 = 0.67; R. Parsley, P. Barboza, and D. Gustine unpublished data) derived from red blood cells, muscle, and urine samples from wild and captive *Rangifer* sp. to estimate the $\delta^{15}N_{Body}$ from $\delta^{15}N_{Creatinine}$:

$$\delta^{15}N_{Body} = (\text{slope} \times \delta^{15}N_{Creatinine}) + \text{intercept},$$

where slope = 0.57 ± 0.42 ($\bar{x}$ ± SD) and intercept = 5.64 ± 0.32‰.

Estimating changes in core body tissues — We corrected the changes in body mass of individuals for mass gains associated with development of concepta (i.e., fetal

and uterine tissues) from capture to the period of urine sampling. We used the birth mass of each female's calf to estimate the mass gained in concepta. We weighed calves for 30 of the 31 penned mothers with repeated estimates of body mass during the urine sampling period; the remaining calf was killed or scavenged shortly after birth in the predator exclosure, so we used the average birth mass of all the calves as an estimate for this calf. We assumed the following: 1) uterine tissue equaled 22% of the birth mass of the calf (Oftedal 1985); 2) 80% of fetal investment occurred during the last trimester of a 230-d pregnancy (Robbins and Robbins 1979, Ropstad 2000); and 3) increases in concepta mass were approximately linear during the latter half of the last trimester (i.e., the period the caribou were in the pen; Robbins and Robbins 1979, Oftedal 1985). Daily gains in reproductive tissues during the last trimester were calculated for each female, multiplied by the number of days between the dates of capture and urine sampling, and then subtracted from each individual's body mass at the time of urine sampling. We averaged the measurements of the "corrected" body mass over the period of urine sampling (BM_{cor}). We divided the body mass at capture by the BM_{cor} to identify whether an animal was gaining or losing core body tissue in the exclosure (core mass change, CMC).

Simulation model — We developed a simulation model to estimate *p*-UN and its plausible range for each urine sample (**APPENDIX C**: Fig. C.1). A simulation model was necessary because errors can potentially accumulate from measures of $\delta^{15}N$ and the variances associated with each discrimination factor or relationship used to estimate the $\delta^{15}N$ in caribou (e.g., Wolf et al. 2009). We developed a spreadsheet-based model that used the observed errors, means, and standard deviations to create distributions for each parameter ($\delta^{15}N_{Diet}$, $\delta^{15}N_{Urea}$, and $\delta^{15}N_{Body}$); selected a random sample (with replacement) from these distributions; stored the estimated *p*-UN for each iteration; and repeated the simulation 10,000 times. For the error associated with estimating each $\delta^{15}N$ via IRMS, we assumed the error was drawn from a uniform distribution that was bounded by the measured $\delta^{15}N \pm 0.39‰$ (error associated with estimating $\delta^{15}N$ of peptone, $n = 149$). To estimate the discrimination factors (Δ_{Urea} and Δ_{Fiber}) and components of the linear equation used to estimate $\delta^{15}N_{Body}$ for each iteration, these parameters were sampled from

a uniform triangular distribution (i.e., upper and lower bounds were equidistant from midpoint; Firko and Podleckis 2002) that was bounded by the 95% confidence interval. We used the mean and standard deviation of $\delta^{15}N_{Fiber}$ for 23 and 30 April (0.99 ± 0.22‰) and the Box-Mueller scheme (Hilborn and Mangel 1997) to generate an estimate of $\delta^{15}N_{Fiber}$ for each iteration of the model for each urine sample.

We used the output from the simulation model to identify potential outliers and estimate the *p*-UN for each urine sample (individual level) and for the penned population (population level). We excluded urine samples with *p*-UN values that did not include 0 or 1 (e.g., median = 1.46; range = 1.01 to 1.90) or those with an absolute range ≥1 (e.g., median = 0.50, range = -1.25 to 1.25). To estimate the *p*-UN at the individual level, we used the simulated range of *p*-UN values for a urine sample and a threshold of 0.46 (Barboza and Parker 2006) to classify each urine sample as coming from caribou that were in positive (≤0.46) or negative N balance (>0.46). Urine samples with ranges of simulated *p*-UN values that overlapped 0.46 were considered to come from animals at or near zero N balance (maintenance or stasis). To estimate the *p*-UN at the population level, we averaged the simulated-median *p*-UN values across urine samples.

Statistics — We used parametric approaches and descriptive statistics to evaluate changes in diet composition and $\delta^{15}N_{Fiber}$ over time, the relationship between major forages in the diet and $\delta^{15}N_{Fiber}$, and changes in core body mass and protein status. We used analysis of variance to compare the amount of major forages (lichens and ration) in the diet within a collection date and to evaluate the effects of collection date on diet composition within forage groups and $\delta^{15}N_{Fiber}$. Post hoc tests were evaluated with *t*-tests and a Bonferroni's correction to α. We used linear regression and a slope test (Sokal and Rohlf 1995) to examine the change in $\delta^{15}N_{Fiber}$ with the estimated proportion of the major foods in the diet. We report descriptive statistics on the BM_{cor} and protein status at the individual level and used 95% confidence intervals to determine the N status (negative, stasis, or positive) at the population level.

We used a Shapiro-Wilk test (Zar 1999) to evaluate the assumption of normality for all comparisons. Results are reported as means ($\bar{x}$) ± SE unless specified otherwise.

For all statistical analyses we defined $\alpha = 0.050$.

Results

Lichens were the largest fraction (>40%) of the diet consumed by caribou (all $F_{1, 8} > 6.88$, all $P < 0.03$; Fig. 4.2). Consumption of the ration (>25% of the diet) appeared to reduce the amount of lichens in the diet especially on 16 April ($F_{1, 8} = 0.02$, $P = 0.91$). The proportion of lichens and ration in the diet changed across sampling times (both $F_{3, 16} > 5.35$, both $P < 0.01$), but occurrences of other forage groups did not vary across sampling periods (all $F_{3, 16} < 1.86$, all $P > 0.18$). The amount of lichens and ration in the diet changed from 9 April to 16 April (both $P < 0.01$; Fig. 4.2), but did not differ among the remaining periods (all $P > 0.05$).

The $\delta^{15}N_{Fiber}$ varied with date of collection ($F_{3, 16} = 8.29$, $P = 0.002$), increasing from 9 April to 16 April ($P = 0.001$) and then stabilizing for the remaining sampling periods ($P > 0.05$; Fig. 4.3). The proportion of lichens and ration in the diets was correlated with $\delta^{15}N_{Fiber}$ (lichens, $r = -0.62$; ration, $r = 0.71$) and the directions of the effects were as expected: $\delta^{15}N_{Fiber}$ decreased as animals consumed more lichens (-0.08 ± 0.05; slope ± 95%CI) and increased with consumption of the ration (0.10 ± 0.05; Fig. 4.4).

Changes in the body mass of caribou were primarily due to the development of concepta. At capture (29 March to 2 April), pregnant caribou ($n = 50$) weighed 122.8 ± 10.8 kg. Body mass was recorded for 31 of 50 caribou during the period of urine sampling (24-27 April). Calves (9.2 ± 1.2 kg) were born 19 May ± 4.7 d ($n = 49$) and, consequently, caribou were estimated to have gained $3.0 \text{ kg} \pm 0.4$ kg of concepta over 25.6 ± 1.3 d in the pen. Some pregnant caribou (26% or 8 of 31 animals) lost body mass from the time of capture, but on average, individuals gained body mass ($2.6 \pm 3.8\%$ of capture mass) in the exclosure during this 4-week period. However, when changes in body mass were corrected for gains in reproductive tissue, 55% of the caribou lost core body tissue and 45% gained core body tissue. Consequently, on average, caribou appeared to maintain their core tissues (mean CMC = 1.00 ± 0.04) albeit with a large

range among individuals (0.94-1.14, min-max).

The isotopic evidence suggested that some caribou in the pen were experiencing N deficits. As expected, the $\delta^{15}N_{Urea}$ was lower (-1.28 ± 1.03‰, $\bar{x}$ ± SD; -2.88 to 0.77‰, range) than the $\delta^{15}N_{Body}$ (2.69 ± 0.66‰; 1.45 to 4.50‰) but typically enriched over the $\delta^{15}N_{Diet}$ by 1.07 ± 1.03‰ (-0.53 to 3.12‰). Based on the range of simulated *p*-UN values, we considered one sample an outlier and removed it from analysis. Regarding the *p*-UN at the individual level, 54% of the urine samples had simulated ranges >0.46 (i.e., the threshold for negative N balance), 46% had estimates that overlapped 0.46 (stasis), and no simulated ranges were ≤0.46 (positive N balance). Similarly, the *p*-UN at the population level suggested that the N balance of the population of caribou in the exclosure was negative (0.67 ± 0.08, $\bar{x}$ ± 95% CI).

Discussion

Despite being provided a relatively high-protein feed, lichens dominated the diets of penned caribou and a majority of the animals were experiencing N deficits. Free-ranging reproductive females in the CH likely experienced more severe protein restrictions during this period. Reproductive females are particularly sensitive to foraging conditions in late winter. The availability of body proteins for reproduction may provide the mechanistic link between environmental conditions, investment in offspring, and population productivity (Chan-McLeod et al. 1999, Lesage et al. 2001, Forchhammer et al. 2002, Bårdsen et al. 2008, McArt et al. 2009). Winters with deep snow affect maternal investment of caribou by reducing birth mass of offspring (Adams 2005) which would have direct implications for recruitment (Adams et al. 1995, Hegel et al. 2010).

Diets of penned caribou: microhistological and isotopic assessments

Females in the exclosure consumed lichens and mosses even though animals were provided a complete ration (Fig. 4.2). The value of lichens as winter forage for *Rangifer* sp. is well documented (e.g., Russell and Martell 1984, Russell et al. 1993, Storeheier et al. 2002a). Lichens comprise >50% of the diets of the Denali (Boertje 1990), Western Arctic (Joly et al. 2007), and Porcupine caribou herds (Russell et al. 1993) in Alaska and

of woodland caribou in Yukon (Fischer and Gates 2005). A mixed diet of lichens and vascular plants may provide the rumen biota with a highly fermentable substrate and enough N for the continued synthesis of microbes (Ørskov 1992, Storeheier et al. 2002b).

Isotopic and compositional changes in the diets of penned caribou were reflected in $\delta^{15}N_{Fiber}$. Lichens are typically depleted relative to atmospheric N in northern systems (Barnett 1994, Ben-David et al. 2001, Finstad 2008). The $\delta^{15}N$ of lichens was highly variable (Table 4.1), but generally low (-6.8 to 0.9‰, range). The addition of a relatively enriched diet item with low variance in $\delta^{15}N$ (ration, Table 4.1) reduced the isotopic diversity of the diet and, consequently, may have enhanced the correlation between diet composition and $\delta^{15}N_{Fiber}$. Measuring $\delta^{15}N_{Fiber}$ was necessary to estimate $\delta^{15}N_{Diet}$ and, subsequently, estimate *p*-UN; however, with further investigation, $\delta^{15}N_{Fiber}$ could be useful in determining the composition of herbivore diets (Fig. 4.4).

The isotopic proxy for diet N ($\delta^{15}N_{Diet} = \delta^{15}N_{Fiber} - \Delta_{Fiber}$) in the model to estimate *p*-UN may have been sensitive to changes in rumen biota that accompanied the formulated diet. Fecal samples of other ruminants are typically enriched 0.4 to 3.3‰ relative to the diet (Steele and Daniel 1978, Sutoh et al. 1987, Sponheimer et al. 2003). Enrichment factors of feces can result from protein-precipitating compounds, intestinal tissue, undigested plant fiber, or rumen biota (Van Soest 1994). The enrichment of indigestible plant matter in the rinsed feces above the diet is likely due to ruminal flora or fauna that escaped acid digestion and intestinal uptake (e.g., fungal hyphae and bacteria that invaded the plant cell walls) as well as microbial contributions from the cecum and large intestine. It is likely that the ruminal community changed (Sundset et al. 2009) when caribou were provided with a highly digestible (81%, Barboza and Parker 2006) formulated ration in the exclosure, but we do not know if those changes affected Δ_{Fiber}. Values for Δ_{Fiber} directly affect estimates of *p*-UN. For example, if we overestimated Δ_{Fiber} by >1.5‰, then the *p*-UN would indicate a positive N balance. We believe our estimates of Δ_{Fiber} were valid, however, because: 1) animals were fed the ration for 4 weeks prior to the collection of feces used to estimate *p*-UN; 2) the estimates of Δ_{Fiber} were derived from studies that included both the formulated ration and lichens; and 3) the

estimates of $\delta^{15}N_{Diet}$ were in the expected range of primary forages. Additionally, estimates of *p*-UN at the individual level incorporated uncertainty in Δ_{Fiber} and corresponded well with CMC that was estimated from changes in body mass while caribou were in the pen.

Isotopic model of N balance

The $\delta^{15}N_{Urea}$ of penned caribou was indicative of animals reallocating or catabolizing body protein. With the exception of *Rangifer* sp. (Parker et al. 2005, Barboza and Parker 2006), there are few data on the $\delta^{15}N_{Urea}$ in ruminants and to our knowledge there are no reported values from wild populations. Although variable, the $\delta^{15}N_{Urea}$ of the penned caribou was similar to whole urine from caribou in the Western Arctic herd: -4 to -2‰ (Finstad 2008). The pool of urea N in the body is a mix of dietary and body N that turns over every 9-12 hours (Barboza and Parker 2008). Dietary inputs to the body pool of urea are primarily through catabolism of amino acids, which is modified by formation of ammonia and by other microbial exchanges of N (Morrison 2000). Reserves of body protein are primarily derived from skeletal muscle (Gerhart et al. 1996) and are typically enriched over diet N (Kelly 2000). At low N intakes and negative N balances, the circulating pool of free amino acids and urea N becomes increasingly enriched as N-bearing substrates are derived more from endogenous sources (Table 4.1; Barboza and Parker 2006). The $\delta^{15}N_{Urea}$ of caribou in the exclosure was enriched over the $\delta^{15}N_{Diet}$ which suggests high contributions from body N.

The estimates of N balance for caribou in the exclosure were contrary to our expectations. We expected female caribou in the exclosure to adapt quickly to the formulated diet and experience a positive N balance. Instead, as indexed by the *p*-UN at the individual and population levels and by CMC, some caribou in the exclosure were experiencing N deficits in late April. The percentage of caribou in the exclosure that were in negative N balance (54%) corresponded closely to the percentage of animals in the exclosure that lost core body tissue (55%). There also were caribou in the exclosure that appeared to gain core body tissue, but gains in body tissues could have been masked

by the changes in the mass of ingesta (e.g., Adamczewski et al. 1987) during a period when dry matter intakes may have increased (Barboza and Parker 2008). Pregnant *Rangifer* sp. in captivity on *ad libitum* feeding schedules can experience negative N balances in late winter when they mobilize reserves of body protein for the N demands of fetal growth (Barboza and Parker 2008). Therefore, we should have expected that wild, pregnant caribou that were given a formulated ration in the exclosure would experience similar constraints. Pregnant females are most likely well adapted to the typically N-restricted environment of late winter. However, the capacity of females to endure late winter conditions and reproduce depends, in a large part, on the interaction of previous reproductive demands (Adams and Dale 1998, Cook et al. 2004) as well as environmental conditions throughout the year (Albon et al. 1987, Forchhammer et al. 2002, McArt et al. 2009) that affect rates of anabolism and catabolism of body tissues (Parker et al. 2009).

Although some reproductive females may have difficulty addressing the N demands of late gestation and lactation, reproduction per se does not necessarily oblige caribou to reallocate body protein to produce a fetus in late winter. Under mild winter conditions, caribou may spare body protein, preferentially deposit dietary N in fetal tissue (Barboza and Parker 2008), and possibly deposit body protein in late winter (Barboza and Parker 2006). Alternatively, poor environmental conditions that affect the rates of anabolism and catabolism of body tissues (Parker et al. 2009) could predispose individuals to rely more heavily on reserves of body protein for survival, and, subsequently, reduce the availability of body protein for reproduction (Barboza and Parker 2008). For example, Adams (2005) observed a decline in the birth masses of calves and Hegel et al. (2010) noted declines in recruitment after severe winters. Indeed, birth masses of caribou calves have been positively correlated with stores of maternal protein (Allaye-Chan 1991). In captive populations of reindeer, however, animals that experienced identical environmental conditions and were fed the same summer and winter diets exhibited varied nutritional responses during winter (Barboza and Parker 2006). A majority of caribou (>50%) in the exclosure were in negative N balance, while some individuals probably experienced gains in body protein.

Considerations for isotopic modeling in ungulates

Determining the protein status of ungulate populations in late winter could be an effective tool to identify nutritional mechanisms that contribute to population changes. The *p*-UN estimates the reliance of an animal on protein reserves to meet physiological demands, whether those demands are reproduction, maintenance, growth, or survival. Restrictions in food availability or quality decrease the resources available for reproduction (e.g., McCullough 2002, Barboza et al. 2009) and, therefore, can precipitate population changes (Skogland 1985, Allaye-Chan 1991). Late winter is an appropriate target to estimate *p*-UN for northern ungulates because of predictable snow cover for collection of urine; less diverse diets (Larter and Gates 1991, Russell et al. 1993, MacCracken et al. 1997, Larter and Nagy 2004), and, consequently, possibly less variation in $\delta^{15}N_{Diet}$; body condition of non-reproductive individuals is approaching annual minima (Adamczewski et al. 1997, Chan-McLeod et al. 1999, Barboza et al. 2004); and demands of gestation are increasing for reproductive females (Oftedal 1985). This non-invasive, isotopic approach has promise for helping to quantify and interpret the consequences of protein restrictions to populations of ungulates, but several important considerations should be addressed prior to applying the approach to other ungulates: species-specific discrimination factors, uncertainty in model parameters, and the challenges of establishing inferences on protein status of a population from random collections of excreta samples.

Discrimination factors (Δ_{Urea} and Δ_{Fiber}) may not be similar between species of ungulates. Differing physiological (e.g., urea recycling) or biological (e.g., composition of rumen biota) mechanisms for a particular species may alter metabolic pathways for various pools or sources of N and this would affect patterns of isotopic enrichment or depletion (Karasov and Martinez del Rio 2007). As observed for discrimination factors in other isotopic models (Caut et al. 2009), the estimates of *p*-UN are highly sensitive to changes in discrimination factors, particularly Δ_{Urea} (D. Gustine, unpublished data). For example, research on captive caribou (Parker et al. 2005), reindeer (Barboza and Parker 2006; 2008), and muskoxen (Gustine et al. 2010) in Alaska suggests that estimates of

Δ_{Urea} may vary slightly by species (Δ_{Urea}: *Rangifer* sp. $n = 15$, 2.35 ± 0.89; muskoxen, $n = 6$, 2.90 ± 0.73). The simulation model and corresponding estimates of *p*-UN at both the population and individual levels attempts to account for uncertainty in Δ_{Urea}; however, it is critical to ascertain species-specific estimates, especially if factors, such as Δ_{Urea}, also change with protein demands or availability. Until current knowledge on Δ_{Urea} improves, either simulation-type approaches will need to be used, such as the one we used here, or possibly a proxy of protein status that may not require a discrimination factor (e.g., the difference between $\delta^{15}N_{Body}$ and $\delta^{15}N_{Urea}$).

The variance associated with estimating the dietary input of the model and the isotopic distance between the model endpoints will affect the ability of the model to reliably detect animals that are in positive N balance. In caribou, variation around the discrimination factor for estimating $\delta^{15}N_{Diet}$ from fecal fiber (Δ_{Fiber}) was greater than that of the linear regression used to estimate the $\delta^{15}N_{Body}$. Subsequently, as the $\delta^{15}N_{Urea} - \Delta_{Urea}$ term approached the $\delta^{15}N_{Diet}$, the error term increased in the simulation model used to estimate *p*-UN. Consequently, a large portion of our "maintenance" or "stasis" samples could have been in positive N balance but, due to this artifact of model uncertainty, we were unable to detect when these caribou were gaining body proteins (*p*-UN ≤ 0.46). This asymmetrical error becomes more important as the difference between the $\delta^{15}N_{Diet}$ and $\delta^{15}N_{Body}$ decreases (i.e., slope of the model increases, Fig. 4.1), and the corresponding estimates of *p*-UN become more sensitive to small changes in model parameters. Consequently, given the current uncertainty in model parameters, this isotopic approach may be unreliable for ungulates that shift from depleted to enriched diets (e.g., graminoids, Finstad 2008), low $\delta^{15}N_{Body}$, and (or) isotopically diverse diets in the winter (i.e., high SD for $\delta^{15}N_{Diet}$).

Different age and sex classes of an ungulate population are nutritionally distinct. The reproductive and non-reproductive components of a population undergo different nutritional trajectories in late winter and this poses challenges to interpreting *p*-UN. In late winter, non-reproductive animals may comprise a large segment of a population and these animals have reduced N demands when compared to reproductive females. Short-

yearlings, males (Ouellet et al. 1997, Barboza and Bowyer 2001), and non-pregnant females (Chan-McLeod et al. 1999, Barboza and Parker 2006) can gain lean mass from late winter to early spring. Therefore, the estimate of *p*-UN at the population level should be considered a conservative estimate of N status because the proportion of reproductive females in a population is commonly <50% (e.g., McCullough 2002). A technique to differentiate pregnant and non-pregnant samples would dramatically increase the sensitivity of this metric as a nutritional indicator as well as the ecological value of this type of isotopic monitoring. However, urinary progesterone concentrations in relation to creatinine did not distinguish pregnant females, non-pregnant females, and adult males in captive caribou during winter (P. Barboza and J. Addison, unpublished data).

We presented 2 approaches to estimate the N status of caribou in the exclosure: population and individual level. Both approaches used a simulation model to incorporate uniform error and approximately normal distributions of model parameters and isotopic proxies of diet and body N. Protein status was simulated at the population level to identify outliers ($n = 1$) and maintain the continuous nature of the *p*-UN estimates. At the individual level, we used the entire simulated ranges of *p*-UN and the 0.46 threshold (as defined in Barboza and Parker 2006) to classify each urine sample as belonging to an animal in positive, negative, or maintenance N balance and then estimate the percent of the caribou in the exclosure within each category of N balance. Although there is some uncertainty about the 0.46 threshold that delineates positive and negative N status, the threshold is a conservative estimate for animals in negative N balance (see Fig. 7 of Barboza and Parker 2006). Therefore, caribou in the exclosure with a simulated range of *p*-UN > 0.46 were most likely experiencing N deficits despite the uncertainties associated with model parameters.

Quantifying the dynamics and influences of N status in wild ungulates will greatly enhance our understanding of nutritional influences on population dynamics. Applying this technique at larger scales should incorporate potential variance in protein status among individual animals and assess how this variance changes as populations or segments of a population approach nutritional limitations (i.e., density-dependent or

-independent mechanisms). As we refine and establish components of this isotopic model for other ungulates, this non-invasive approach has the potential to increase our understanding of protein constraints and N balance in ungulates.

Management Implications

Isotopic approaches, such as *p*-UN, could be valuable, non-invasive tools to examine intra- and inter-annual changes in nutrient partitioning for northern ungulates. At a minimum, estimates of *p*-UN at the individual level provide a discrete index of protein status. In spite of being provided natural and formulated forages, pregnant caribou were challenged to meet their protein requirements. Reproductive females are the most sensitive demographic group to protein restriction in late winter; therefore, if possible, isotopic assessments of protein status should focus on this component of a population. More likely, estimates of protein status from simple, random collections of excreta provide a conservative measure of nutritional challenges in late winter. With appropriate quantification of species-specific model parameters, this non-invasive technique could be applied at various spatial and temporal scales to assess trends in the protein status of free-ranging populations of northern ungulates. Intra- and inter-annual estimates of protein status could help managers monitor the effects of foraging conditions on nutritional constraints throughout winter, increase the efficiency and efficacy of management actions (e.g., vegetation and predator management), and help to prepare stakeholders for potential changes in population trends.

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Table 4.1. Composition of the pelleted ration and lichens that were fed to female caribou ($n = 50$) from the Chisana Herd, YT, Canada, April 2006.

Characteristic	Ration[a] ($n = 5$)		Mixed lichens[b] ($n = 21$)	
	$\bar{x}$	SD	$\bar{x}$	SD
Nitrogen (%)	2.8	0.15	0.5	0.25
Ash (%)	9.2	0.41	3.0	1.34
Neutral detergent fiber (%)	27.3	1.83	84.2	3.63
Acid detergent fiber (%)	13.8	1.26	13.1	6.75
Lignin (%)	3.4	0.47	4.5	4.06
$\delta^{15}N$ (‰)	1.7	0.35	-2.1	2.3

[a]Barboza and Parker (2006).

[b]Lichen samples were predominantly *Cladina* and *Cladonia* spp. with minor occurrences of *Stereocaulon* spp., *Flavocetraria* spp., *Peltigera* spp., and *Cetraria* spp.

Table 4.2. Parameters used to correct microhistological analyses of feces for differential digestibility of forages in penned caribou from the Chisana Herd, YT, Canada, April 2006.

Major forage groups	Apparent dry matter digestibility ($g \cdot g^{-1}$)	N ($g \cdot g^{-1}$)	
		$\bar{x}$	SD
Deciduous shrubs	0.60[a]	0.010[a]	0.003
Evergreen shrubs	0.64[a]	0.012[a]	0.002
Forbs (includes *Equisetum* spp.)	0.46[a]	0.011[a]	0.003
Graminoids (includes *Carex* spp.)	0.54[a]	0.007[a]	0.001
Lichens	0.70[a]	0.005[b]	0.003
Mosses	0.07[a]	0.009[a]	0.003
Ration	0.81[c]	0.028[a]	0.002

[a]Boertje (1981)

[b]This study.

[c]Barboza and Parker (2006)

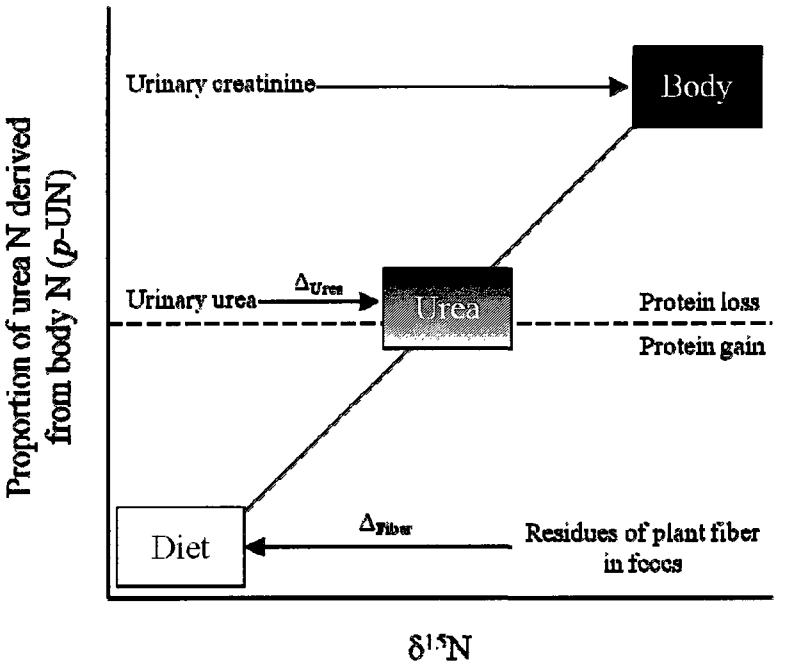

Figure 4.1. Conceptual model for using isotopic ratios of N ($\delta^{15}N$) in excreta to estimate the proportion of urinary urea N that is derived from body N (*p*-UN) to determine N status. The discrimination factors for the creation of urea from dietary N for animals in positive N balance (Δ_{Urea}) and the residues of plant fiber in feces above the $\delta^{15}N_{Diet}$ (Δ_{Fiber}) were derived from captive caribou and reindeer.

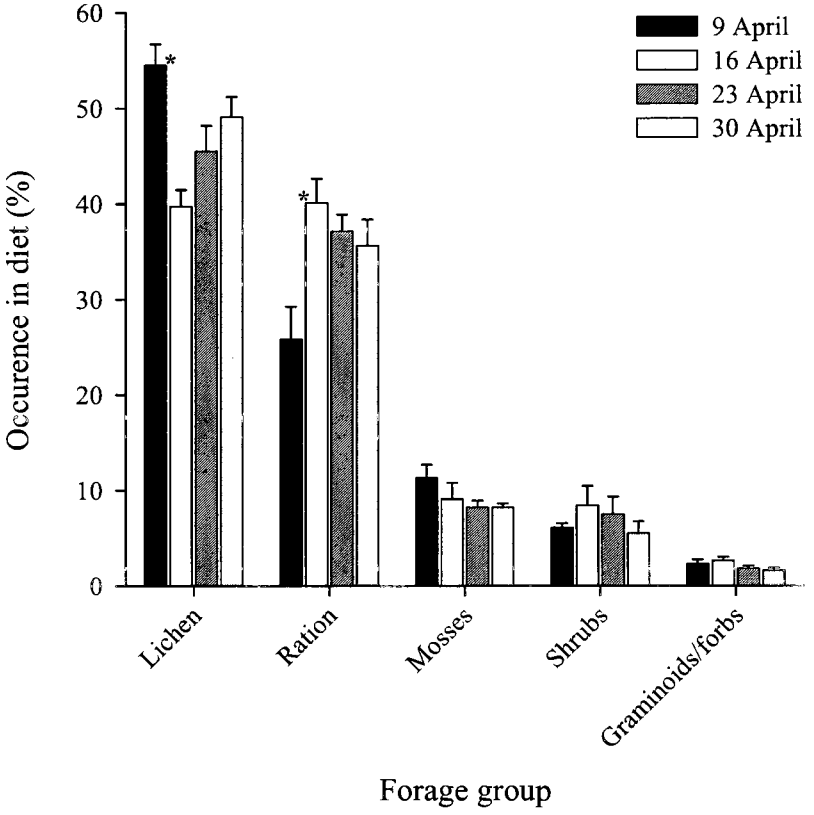

Figure 4.2. Occurrences of forages in the diets ($\bar{x} \pm$ SE) of penned caribou from the Chisana Herd during April 2006; an asterisk denotes significantly different ($P < 0.011$) means within a forage group between sampling periods.

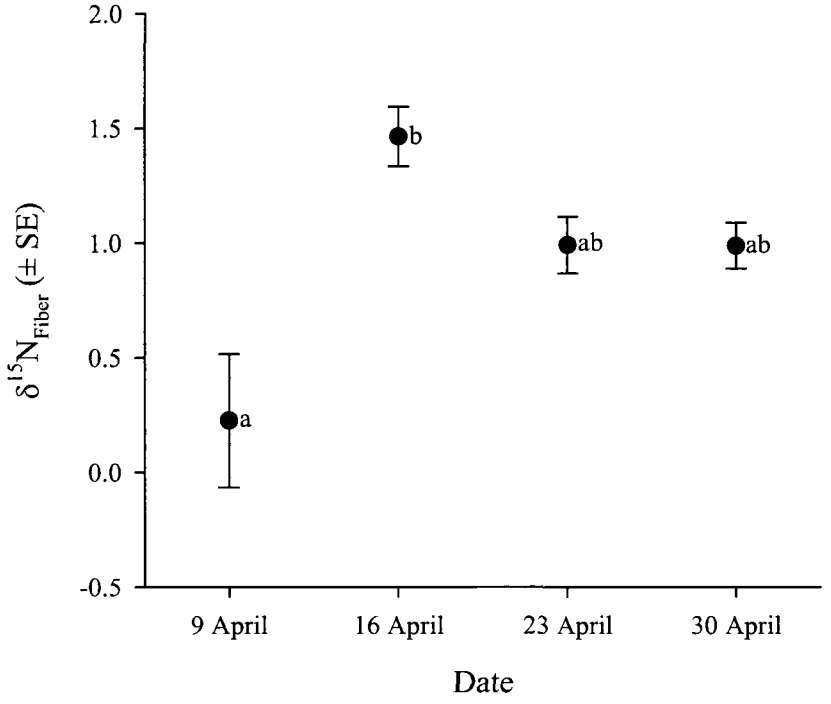

Figure 4.3. The $\delta^{15}N$ of residues of plant fiber in feces ($\delta^{15}N_{Fiber}$) collected from penned caribou in the Chisana Herd, by date in 2006; different letters denote a significant difference between means ($P = 0.001$).

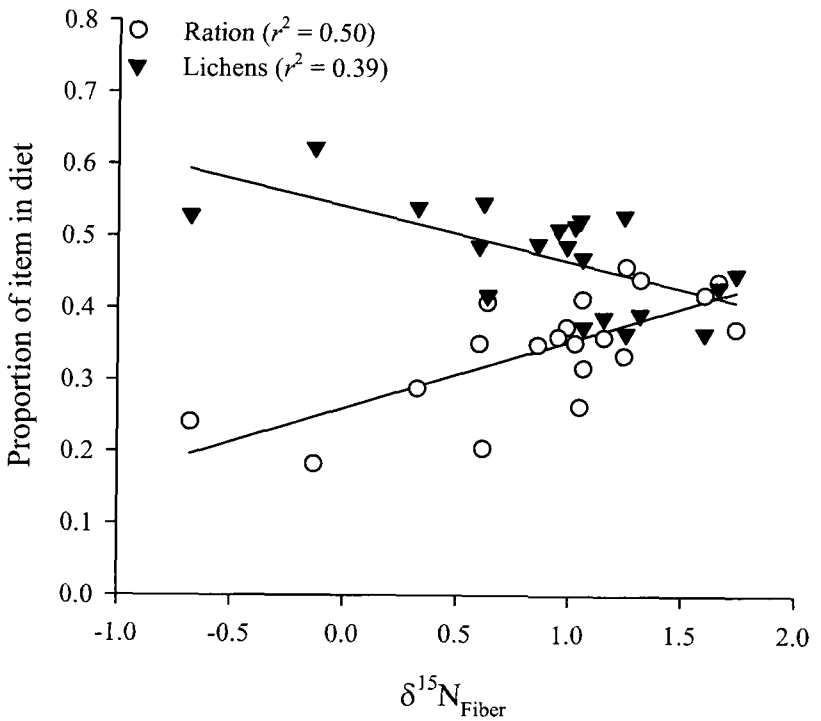

Figure 4.4. Proportions of the formulated ration and lichens in the diet in relation to the $\delta^{15}N$ of residues of plant fiber in feces ($\delta^{15}N_{Fiber}$) from penned caribou of the Chisana herd, April 2006.

CHAPTER 5 - DIVERSITY OF NITROGEN ISOTOPES AND CORRELATES OF PROTEIN STATUS IN CARIBOU: IMPLICATIONS FOR MONITORING NORTHERN UNGULATES[a]

Abstract

Nutritional condition is an important determinant of productivity and survival in caribou [*Rangifer tarandus* (Linnaeus, 1758)]. We evaluated diets, 2 isotopic proxies of protein status for 2 ecotypes of caribou in 4 herds in late winter (2006-2008) by using samples of excreta (n = 1,150) and isotopes of nitrogen (N; urea, dietary, and body). Diets were dominated by lichens and mosses (>70%), while isotopes of N and estimates of protein status were diverse between ecotypes and among herds. The δ^{15}N of urinary urea was typically low but highly variable (-4.68 ± 2.67‰, $\bar{x}$ ± SD). Dietary N also had low δ^{15}N (-4.18 ± 0.92‰) whereas body N was generally more enriched (2.20 ± 1.56‰) than urea or the diet. A portion of the observed variance in estimated protein status (r^2 = 0.26) could be explained by the proportion of shrubs in the winter diet. Although there is value to using isotopes of N in feces and urine as a non-invasive tool for evaluating protein status in northern ungulates, considerable analytical and sampling challenges remain in applying isotopic approaches at large scales.

Introduction

The attention given to monitoring northern ungulates has increased with concerns about the projected patterns of warming as well as the rate of industrial development at high latitudes (National Research Council 2008). Caribou and reindeer [*Rangifer tarandus* (Linnaeus, 1758)] are a circumpolar species that inhabits forests and tundra from coasts to mountain ranges over a large latitudinal gradient (50 to 80° N; Blix 2005). Caribou are an important indicator species due to their sensitivity to natural (e.g.,

[a]Gustine, D. D., P. S. Barboza, J. P. Lawler, L. G. Adams, K. L. Parker, S. M. Arthur, and B. S. Shults. Diversity of nitrogen isotopes and correlates of protein status in caribou: implications for monitoring northern ungulates. Prepared for Canadian Journal of Zoology.

wildfire, Schaefer and Pruitt 1991) and anthropogenic disturbances (e.g., road development, National Research Council 2003, Johnson et al. 2005) and their value as a subsistence resource for rural communities (Hummel and Ray 2008). Consequently, resource management agencies in North America and Eurasia are tasked with monitoring the status and trends of caribou populations. Challenges of monitoring include establishing adequate baseline conditions and identifying population parameters that are cost effective and indicative of population trajectories (Klein et al. 2005).

The nutrition of individuals is an important determinant of productivity in caribou (Dauphiné 1976, Cameron and Ver Hoef 1994, Adams and Dale 1998, Parker et al. 2009). High seasonal variation in plant abundance in the north accentuates the need for caribou to replenish stores of fat and protein (Oftedal 2000) during a short growing season for winter survival (Chan-McLeod et al. 1999, Barboza and Hume 2006, Parker et al. 2009). The ability to acquire adequate fat stores helps meet the energetic rigors of winter (Adamczewski et al. 1987), while the dynamics and availability of body protein may be a critical constraint for reproduction (Barboza and Parker 2008). Body stores of non-reproductive caribou approach annual minima in late winter (Chan-McLeod et al. 1999, Barboza et al. 2004) whereas reproductive females continue to bear the additional nutritional costs of gestation (Oftedal 1985). Thus, incorporating assessments of energetic or protein status of individual animals in late winter would aid in the monitoring and management of populations (Franzmann 1985). Most methods for assessing aspects of nutritional condition, however, require the capture (Stephenson et al. 1998, Cook et al. 2001) or killing of individuals (Gerhart et al. 1996). Although clearly valuable, application of these techniques may be limited by logistic difficulties and financial costs of working in remote areas, or precluded by biological (e.g., small populations), legal (e.g., conservation units), and cultural (e.g., subsistence use) considerations.

Currently, excreta-based techniques (i.e., ratio and isotopic composition of urinary metabolites) are the only non-invasive approaches to sample the nutritional status of individual caribou in remote areas during winter. The ratios of urinary metabolites

(allantoin, cortisol, glucaronic acid, potassium, and urea) in snow relative to creatinine have been used with mixed success (see review in Parker 2003) to evaluate various metrics of condition in ungulates (DelGiudice et al. 1989, Saltz and White 1991, Parker et al. 1993, DelGiudice et al. 2000, Servello and Schneider 2000, Larter and Nagy 2001, Säkkinen et al. 2001). For caribou and reindeer, some ratio-based approaches may be confounded by changes in renal function that affect excretion rates of urinary urea and creatinine (Säkkinen et al. 2001, Parker et al. 2005).

Isotopes of nitrogen (N) in feces and urine can be used to assess protein status in caribou by evaluating relative contributions of body protein and dietary N to urinary urea N (Barboza and Parker 2006, Gustine et al., *in press*). Urea in urine is derived from two sources of N: dietary and body proteins (Fig. 5.1). Dietary proteins are typically depleted in ^{15}N compared to body proteins (Kelly 2000, Caut et al. 2009). As animals rely more heavily on body proteins to meet metabolic demands, the $\delta^{15}N$ of urea increases (Barboza and Parker 2006). With estimates of $\delta^{15}N$ of diet and body proteins, a linear-mixing model (Karasov and Martinez del Rio 2007) can be used to estimate the contributions of N from the diet and the body to urea (Barboza and Parker 2006). Urinary creatinine is a muscle metabolite from which the $\delta^{15}N$ is used to estimate the $\delta^{15}N$ of red blood cells (body proteins). Fractions of plant fibers in fecal samples can be used to estimate $\delta^{15}N$ of the diet (Gustine et al., *in press*).

Caribou demonstrate considerable behavioral and physiological plasticity to surviving and reproducing in northern environments. Behavioral adaptations are primarily in response to changes in food availability and the risk of predation (e.g., migratory and sedentary ecotypes; Bergerud 1996). For migratory populations of caribou that range over large annual areas and commonly occur at high localized densities, population trajectories have often been linked to forage resources (e.g., Couturier et al. 2009). Conversely, sedentary populations use smaller annual ranges, occur at lower densities, and are typically less constrained by forage availability but suffer heavy predation on neonates (Adams et al. 1995, Jenkins and Barten 2005).

We present the first attempt to apply isotopic approaches using N signatures in

urine and feces to assess protein status of free-ranging caribou including migratory [Central Arctic (CAH) and Western Arctic (WAH) herds] and sedentary [Denali (DH) and Chisana (CH) herds] ecotypes. Our objectives were to provide an understanding of the nutritional status of individuals in these herds; to establish a baseline for monitoring efforts in these populations; and to identify and discuss any potential nutritional constraints or correlates by ecotype or herd. We collected fecal and urine samples from foraging sites for each herd during late winter from 2006 to 2008. We used microhistology of fecal samples to estimate the composition and diversity of caribou diets in late winter. Isotopic ratios of $^{15}N/^{14}N$ in urinary urea, the diet (from feces), and body N (from urinary creatinine) were used to estimate 2 proxies of protein status. We compared characteristics of foraging sites, isotopic parameters, and proxies of protein status by ecotype, herd, year, and foraging site. Additionally, characteristics of foraging sites were used to explain the observed variance in each proxy of protein status. We discuss the implications and challenges of employing this non-invasive isotopic approach to assess protein status of an ungulate population that ranges over potentially large and diverse environments.

Methods

Study areas

Groups of caribou were sampled in the east-central Brooks Range in northern Alaska (CAH); along the Kobuk River and in the Nulato Hills of western Alaska (WAH); in the Wrangell-St. Elias Ranges of Alaska and the Yukon Territory (CH); and on the north slope of the Alaska Range in central Alaska (DH; Fig. 5.2). Wintering areas for each herd have been described as follows: CAH (Cameron and Whitten 1979, Fancy et al. 1989, Lenart 2007), WAH (Dale et al. 1994, Ballard et al. 1997), CH (Farnell and Gardner 2002, Gustine et al., *in press*), and DH (Adams et al. 1995, Adams 2005).

Sample collection and processing

Samples of excreta were collected during late winter from foraging sites used by 4

populations of caribou (Table 5.1). We focused sampling efforts in the wintering areas of radio-collared female caribou where access by aircraft (fixed wing or helicopter) or snow machine was feasible. Sampling sites (also referred to as foraging sites) were areas where groups of caribou had recently foraged or bedded (as determined from presence of caribou, timing of last snowfall, or condition of foraging craters). We assumed that excreta samples were from unique animals and that the sampled sites were independent replicates of each herd for that year of collection. We distributed excreta sampling over the estimated extent of each foraging site (~200 to 1,000 m) as in DelGiudice et al. (1989) and assumed that excreta samples collected within each foraging site were from different animals. The location of the approximate center of the foraging site was recorded with a global positioning system.

Recently voided and discrete samples of urine in snow (urine; approx. 100 ml) and feces (approx. 15 g) were collected into plastic bottles or bags with leak-proof seals. We used an axe, knife, trowel, or the collection bottle to assist in collecting the most concentrated portion of each urine sample. Collection tools were cleaned after each collection and samples were stored at -20°C for processing. To concentrate the urinary metabolites for isotopic analysis, we lyophilized the urine samples. Freeze-dried urine was rehydrated to 3.6 ml with distilled water and frozen in cryovials. Urinary urea and creatinine were isolated and collected by steam distillation and high performance liquid chromatography (HPLC), respectively (Nolan and Leng 1972, Xue et al. 1988, Barboza et al. 1997, Barboza and Parker 2006). Samples of urinary metabolites that were low in either urea or creatinine N (<1.4 micromoles) were excluded from the analysis because they were below the sensitivity of the mass spectrometer.

Feces were used to estimate diet composition, diet diversity, and $\delta^{15}N_{Diet}$. We dried fecal samples to a constant mass in a forced-air oven at 50°C. A composite sample of feces was created for each foraging site to estimate the proportion of plants within forage groups in the diet. Composite samples (Table 5.1) were created by randomly selecting 5-10 pellets from each fecal sample collected at a site. The Wildlife Habitat Nutrition Laboratory (Washington State University, Pullman, Washington) performed the

microhistological analyses on the composite samples (plant species >5% in diet at 150 views). We used the apparent dry matter digestibility of forage groups for caribou (Boertje 1981) to correct the relative density of plant fragments for the differential digestion of forages (Leslie et al. 1983). Diet composition was estimated for the following major groups of forage in the diets of caribou: lichens, mosses, graminoids (sedges and grasses), forbs (including *Equisetum* spp.), evergreen shrubs, and deciduous shrubs. The Shannon-Wiener Index (H'; Krebs 1989) was used to estimate the diversity of the diet from the reconstructed diets of the foraging sites. As in Gustine et al. (*in press*), we isolated and measured the $\delta^{15}N$ of residues of plant fibers from individual fecal samples ($\delta^{15}N_{Fiber}$) to estimate $\delta^{15}N_{Diet}$.

Characteristics of foraging sites

We used spatial data and a GIS (Environmental Systems Research Institute, Redlands, California) to estimate physiographic characteristics of foraging sites. We estimated elevation (m) and derived slope (°) from digital elevation models (DEM) from the U.S. Geological Survey (1999) and the Yukon Territorial Government (2009). A vector ruggedness measure was estimated at the fine (0.18 km) and coarse (1 km) scale (Sappington et al. 2007).

To minimize the number of comparisons among correlated variables of diet and terrain and reduce the number of parameters in the models to evaluate protein status (Gotelli and Ellison 2004), we used standardized principal component scores from the first (PC1) and second (PC2) axes to create variables for characteristics of diet and terrain for each foraging site. Primary (PC1 diet) and secondary (PC2 diet) characteristics of diet were estimated from the proportion of each forage group in the diet and diet diversity. We derived primary (PC1 terrain) and secondary (PC2 terrain) terrain characteristics from elevation, slope, and vector ruggedness at 2 spatial scales (0.18 and 1 km).

Isotopic indicators of protein status

Isotope ratio mass spectrometry (IRMS) was used to measure $^{15}N/^{14}N$ in excreta

samples against atmospheric N (δ in ‰; Gannes et al. 1997) at the Alaska Stable Isotope Facility (University of Alaska Fairbanks, Fairbanks, AK; UAF), Forest Soils Laboratory (UAF), and the Marine Biological Laboratory (Woods Hole, Massachusetts). These systems were accurate within 0.39‰ of peptone from meat.

We used N metabolites and residues from excreta to estimate 2 isotopic proxies of protein status in caribou. First, the proportion of urea N derived from body N (p-UN; Barboza and Parker 2006) was derived from the following dual-source linear mixing model:

$$p\text{-UN} = (\delta^{15}N_{Urea} + \Delta_{Urea} - \delta^{15}N_{Diet}) / (\delta^{15}N_{Body} - \delta^{15}N_{Diet})$$

The $\delta^{15}N_{Urea}$ is the $\delta^{15}N$ of urea in the samples of urine in snow. The $\delta^{15}N_{Urea}$ in this isotopic mixing model needed to be corrected for changes in $\delta^{15}N$ that occurred when urea was initially formed from dietary sources of N ($\delta^{15}N$ of the diet - $\delta^{15}N$ of urinary urea = Δ_{Urea}). We used Δ_{Urea} from previous research on captive *Rangifer* on formulated diets that were in positive N balance (2.35 ± 0.89‰, $\bar{x}$ ± SD, n = 15; Barboza and Parker 2006; Barboza and Parker 2008; Parker et al. 2005). The $\delta^{15}N_{Diet}$ was determined from residues of plant fibers in feces ($\delta^{15}N_{Fiber}$; Gustine et al., *in press*). To estimate $\delta^{15}N_{Diet}$, we used $\delta^{15}N_{Fiber}$ and a discrimination factor (Δ_{Fiber}) derived from captive *Rangifer* on mixed and 100% lichen diets (Δ_{Fiber} = 3.34 ± 1.17‰, n = 26; D. Gustine, P. Barboza, and J. Addison, unpublished data). To estimate the $\delta^{15}N_{Body}$ from $\delta^{15}N_{Creatinine}$, we used a linear equation (n = 40, r^2 = 0.672; SEE = 0.733) derived from red blood cells, muscle, and urine samples from wild and captive *Rangifer* [$\delta^{15}N_{Body} = (0.57 \times \delta^{15}N_{Creatinine}) + 5.64$; see **APPENDIX B**: Fig. B.1].

We also calculated the difference between $\delta^{15}N_{Body}$ and $\delta^{15}N_{Urea}$ ($\Delta_{Body\text{-}Urea}$) as an additional index of protein status (Fig. 7a in Barboza and Parker 2006, and suggested in Gustine et al., *in press*), because isotopic mixing-models are highly sensitive to discrimination factors (Caut et al. 2009, Wolf et al. 2009) and this metric does not require an estimate of $\delta^{15}N_{Diet}$. We assumed that larger values for $\Delta_{Body\text{-}Urea}$ indicated an adequate supply of dietary protein while lower values indicated an inadequate supply of dietary protein and, subsequently, the catabolism of body protein.

Simulation model to estimate *p*-UN — We estimated *p*-UN for individual urine samples with a spreadsheet-based simulation model (**APPENDIX C**: Fig. C.1) that incorporated errors in discrimination factors (Δ_{Urea} and Δ_{Fiber}) and the end points of the mixing model ($\delta^{15}N_{Diet}$ and $\delta^{15}N_{Body}$; Wolf et al. 2009). The simulation model used the observed errors, means, and standard deviations to create distributions for each parameter. For the error associated with estimating each $\delta^{15}N$ via IRMS, we assumed that the error was drawn from a uniform distribution that was bounded by the measured $\delta^{15}N \pm 0.39‰$ (the accuracy of measuring the peptone standard). The Δ_{Urea}, Δ_{Fiber}, and the parameters used to estimate $\delta^{15}N_{Body}$ were sampled from a uniform triangular distribution (Firko and Podleckis 2002) that was bounded by the 95% confidence interval. We used the means and standard deviations of $\delta^{15}N_{Fiber}$ for each foraging site and the Box-Mueller scheme (Hilborn and Mangel 1997) to generate a different estimate of $\delta^{15}N_{Fiber}$ by foraging site, and therefore $\delta^{15}N_{Diet}$, for each run of the model. Each run of the model selected a random sample (with replacement) from these distributions; stored the estimated *p*-UN for each run; and repeated the run 10,000 times. We used the median *p*-UN value from the 10,000 runs of the simulation model as the estimate of *p*-UN for each urine sample.

Statistical analyses

Parametric and descriptive statistics were used to evaluate diets and protein status by caribou ecotype and herd. We used analysis of variance (ANOVA) and a nested design to evaluate the main effects of ecotype (herd nested in ecotype) on the PC1 of diet and terrain. If there was no effect of ecotype, we examined the main effect of herd (year nested in herd, and foraging site nested in year; Gotelli and Ellison 2004). Analysis of covariance was used to examine the proportion of forage groups in the diet (as indexed by microhistology) on $\delta^{15}N_{Fiber}$ of each foraging site (mean, $\bar{x}$) by ecotype (Zar 1999). Linear regression and confidence intervals (95%) were used to assess the effects (β) of the relationships between the proportions of forage groups in the diet on $\delta^{15}N_{Fiber}$. We used a nested ANOVA to examine the main effect of ecotype (same nested design as

above with urine sample nested in foraging site) on each isotope ($\delta^{15}N_{Urea}$, $\delta^{15}N_{Diet}$, and $\delta^{15}N_{Body}$) and proxy of protein status (p-UN and $\Delta_{Body\text{-}urea}$). If there was no effect of ecotype, we examined the effect of herd (with aforementioned nested factors) on isotopes and protein status. To describe variance of the isotopic parameters across foraging sites ($\delta^{15}N_{Urea}$, $\delta^{15}N_{Diet}$, and $\delta^{15}N_{Body}$), we present the mean ($\bar{x}_{SD}$) and range of the standard deviation ($SD_{Min\ to\ max}$).

Multiple regression (Zar 1999), and the information-theoretic approach (Burnham and Anderson 2002) were used to evaluate correlates of protein status (i.e., p-UN and $\Delta_{Body\text{-}urea}$) with characteristics of foraging sites. The model set ($n = 8$ for each proxy of protein status) included the null model, ecotype, and models derived from primary forages in the diet and characteristics of the diet and terrain (Table 5.2). Foraging sites ($n = 32$) with data for all variables were included in analysis. Conservative tolerance scores (<0.40) were used to evaluate multi-collinearity among the set of independent variables. We used a deviation contrast for the categorical variable (ecotype; Menard 2002). Akaike's information criterion adjusted for small sample sizes (AIC_c) and weights (w_i) were used to evaluate the model set. We used coefficients (β), standard errors adjusted for intra-group correlation (i.e., clustered by foraging site; Huber and Ronchetti 2009), and 95% confidence intervals to evaluate parameters from the models with the lowest AIC_c and most support (as indicated by w_i).

A Shapiro-Francia test (Zar 1999) was used to evaluate the assumption of normality for all comparisons. We defined $\alpha = 0.050$ and used Stata 9.2™ (StataCorp, College Station, TX) for all statistical analysis.

Results

We collected 572 urine and 578 fecal samples from 39 foraging sites (Table 5.1; **APPENDIX E**: Table E.1) in the wintering ranges of 4 caribou herds across 3 years (Fig. 5.2). Thirty-four percent of the urine samples were either too low in N to be reliably estimated by IRMS or were lost to autosampler malfunction in the IRMS; thus, we estimated protein status from 379 urine samples. We estimated the diet composition and

diversity for 37 of the 39 foraging sites (Table 5.3; **APPENDIX E**: Table E.2-E.5) because the amounts of feces collected from 2 sites (Central Arctic 2007, $n = 1$; Chisana 2006, $n = 1$) were insufficient for analysis after samples were analyzed for $\delta^{15}N_{Fiber}$.

Characteristics of diet and terrain did not differ by ecotype or herd (Table 5.4). Lichens typically dominated the diets of migratory and sedentary herds of caribou in all years (68 ± 4.6%, $\bar{x}$ ± 95% CI; 18 to 86%, range; $n = 37$, Table 5.3). However, foraging sites (one per year) from the CAH in 2007 and 2008 had <27% lichen in the diet, compared to >47% lichen in the diets at the remaining foraging sites for all herds. Mosses were generally the second most abundant forage group in the diets (14 ± 2.6%; 9 to 27%; Table 5.3), whereas vascular plants constituted 19 ± 2.8% of the diet (4 to 46%, range). Diversity of the diet increased as the proportion of lichen in the diet decreased (Fig. 5.3). Characteristics of the diet at foraging sites (as indexed by PC1 and PC2, 49% and 23% of variance explained, respectively) were driven primarily by the proportion of lichens and mosses in the diet, diet diversity, and the proportion of evergreen and deciduous shrubs in the diet. Regarding terrain characteristics, PC1 (64% of variance explained) was influenced by slope and both vector-ruggedness measures; PC2 (24% of variance explained) was driven primarily by elevation (Fig. 5.3). The primary components of diet and terrain at foraging sites (PC1) did not differ between ecotypes or among herds (all $P > 0.108$), although there were differences between years within herds for PC1 of diet ($P = 0.023$; Table 5.4).

Except for lichens and graminoids (both $F_{2, 33} > 5.62$; both $P < 0.025$), the proportion of major forages in the diet on $\delta^{15}N_{Fiber}$ did not differ for any forage group (all $F_{2, 33} < 2.63$; all $P > 0.113$); groups of major forages in the diet were poor correlates of $\delta^{15}N_{Fiber}$ (all $F_{2, 33} < 3.89$; all $P > 0.057$). For lichens and graminoids, however, the directions of the effects were as expected (Fig. 5.4): $\delta^{15}N_{Fiber}$ increased with the proportion of graminoids in the diet (0.03 ± 0.017, β ± 95% CI; $R^2 = 0.275$) and decreased with the proportion of lichens (-0.06 ± 0.053; $R^2 = 0.150$).

The range of values for $\delta^{15}N_{Urea}$, $\delta^{15}N_{Diet}$, and $\delta^{15}N_{Body}$ was large (-11.54 to 5.67‰) across herds and years (Fig. 5.5; **APPENDIX E**: Tables E.6 and E.7). Urinary urea

was typically depleted in ^{15}N (-4.68 ± 2.67‰, $\bar{x}$ ± SD; n = 465); it also was the most varied isotopic parameter we measured within each foraging site ($\bar{x}_{SD}$ = 1.88‰; $SD_{Min\ to\ max}$ = 0.51 to 9.23‰). The diet was depleted in ^{15}N (-4.18 ± 0.92‰; n = 578) and was the least varied isotopic parameter we measured within each foraging site ($\bar{x}_{SD}$ = 0.44‰; $SD_{Min\ to\ max}$ = 0.24 to 0.72‰). Conversely, the $\delta^{15}N_{Body}$ was usually heavier in ^{15}N (2.20 ± 1.56‰; n = 437) than either the $\delta^{15}N_{Urea}$ or $\delta^{15}N_{Diet}$ (Fig. 5.5); the $\bar{x}_{SD}$ = 0.82‰ and $SD_{Min\ to\ max}$ = 0.23 to 2.38‰.

The isotopes ($\delta^{15}N_{Urea}$, $\delta^{15}N_{Diet}$, and $\delta^{15}N_{Body}$) and proxies of protein status (p-UN and $\Delta_{Body\text{-}urea}$) did not differ between ecotypes (all $P > 0.217$) or among herds (all $P > 0.092$; Table 5.4). Within herds, however, there were differences between or among years for $\delta^{15}N_{Urea}$, $\delta^{15}N_{Body}$, and p-UN (all $P < 0.048$). All the isotopes (Fig. 5.5) and proxies of protein status (Fig. 5.6a, b) were different among or between foraging sites within each year (all $P < 0.001$; Table 5.4).

Both proxies of protein status were correlated with the proportion of shrubs (deciduous and evergreen combined) in the diet (both $r^2 < 0.27$, both w_i = 1.00; Table 5.2). The amount of shrubs in the diet had a negative effect on p-UN (-4.3 ± 2.05, β ± 95% CI; 0.9 ± 0.34, intercept ± 95% CI) and a positive effect on $\Delta_{Body\text{-}urea}$ (β = 30.4 ± 13.68; intercept = 3.3 ± 2.03; Fig. 5.7); both relationships indicate that protein status generally improved as the proportion of shrubs in the diet increased.

Discussion

Regardless of the apparent behavioral or demographic differences between caribou ecotypes or among herds, ecotype or herd was not a significant factor for characteristics of the diet and terrain, isotopes of N, or proxies for protein status. The extent of the variability in isotopes was unexpected and has important implications to attempting a monitoring program. Small sample sizes and high variance in the isotopes limited our ability to make any inferences from these apparent "similarities" at the ecotype or herd level. We also identified a set of concerns that may prohibit the application of the linear-mixing model approach (p-UN) to some populations of caribou

at large scales. Additionally, there were inter- and intra-annual differences within herds, and some of those differences had implications to the index of protein status ($\Delta_{Body\text{-}urea}$) of caribou.

Diet and terrain

Migratory and sedentary caribou consumed similar diets while foraging at physiographically diverse sites. Typical of continental populations of caribou in North America (e.g., Scotter 1967, Boertje 1984, Russell et al. 1993, Fischer and Gates 2005, Joly et al. 2007), the winter diets of these four caribou herds were composed primarily of lichens and mosses (>70%; Table 5.3). Reductions in consumption of lichens increased amounts of other forages in the diet, and, consequently, the diversity of the diet (Fig. 5.3). A mixed diet of lichens and vascular plants provides a diet high in digestible carbohydrates with enough N and minerals for the continued synthesis of ruminal microbes (Ørskov 1992, Storeheier et al. 2002). Ingestion of moss could be incidental to lichen consumption or may indicate deteriorating range conditions (Ihl 2010). Except for two foraging sites in the CAH (2007 and 2008), the amount of lichen in the diets was generally similar to what has been reported previously (DH = 66 ± 13.4%, Boertje 1984; CH = 58 ± 2.5%, Farnell and Gardner 2002; WAH corrected estimate = 64%, Joly et al. 2007).

Inter-annual differences in the primary characteristics of diet of each herd (PC1 diet; Table 5.4) were likely due to changes in forage availability. Caribou may have foraged in different plant communities and snow conditions may have affected the availability of forages within each community (Adamczewski et al. 1988). Although we did not measure characteristics of vegetation or snow conditions at each foraging site, there were differences in snowfall among years: winter of 2007-08 had more snowfall than the previous two winters for all the herds (National Climatic Data Center 2008). Diet estimates from 2008 had the least amount of lichens and the highest diversity for three of the four caribou herds (Table 5.3).

Patterns in $\delta^{15}N$ of the diet, urinary urea, and body proteins

Diet — Compositional changes of the diets were reflected in $\delta^{15}N_{Fiber}$. Lichens are typically depleted relative to atmospheric N (-21 to 0.9‰; Ben-David et al. 2001, Asada et al. 2005, Finstad 2008, Fogel et al. 2008, Gustine et al., *in press*) whereas graminoids are generally heavier in ^{15}N (-5 to 5‰; Barnett 1994, Schulze et al. 1994, Finstad 2008). The $\delta^{15}N_{Fiber}$ tracked these patterns in the natural abundance of ^{15}N found in lichens and graminoids (Fig. 5.4). However, the relationship between the amount of lichen in the diets and $\delta^{15}N_{Fiber}$ ($R^2 = 0.15$) was weaker than that reported for wild caribou confined to a 12-ha predator exclosure (CH, lichens, $r^2 = 0.39$; Gustine et al., *in press*). The diet in the exclosure was primarily composed of two forages (lichens and formulated ration) that were more homogenous and isotopically distinct.

The capacity of $\delta^{15}N_{Fiber}$ to index the composition of herbivore diets is limited by the spatial variance in $\delta^{15}N$ of each forage group. The $\delta^{15}N$ of vascular and non-vascular plants is dependent on N availability, the $\delta^{15}N$ of the soil, fixation of inorganic N, as well as the depth of the root system (Karasov and Martinez del Rio 2007). These factors vary with season, landscape processes, plant community structure, and microsite characteristics that affect soil properties and N availability (Kielland and Chapin 1992). Consequently, the $\delta^{15}N$ of plants within the same plant and functional group can be highly variable in space and time (Adams and Grierson 2001, Evans 2001, P. E. Matheus, personal communication). Indeed, at the smallest spatial scale, the variation of $\delta^{15}N_{Diet}$ within foraging sites ($SD_{Min\ to\ max}$ = 0.24 to 0.72‰) strongly suggested that caribou at a foraging site were consuming isotopically similar diets, whereas the $\delta^{15}N_{Diet}$ was generally different among foraging sites within each herd and year (Table 5.4). Thus, caribou at different foraging sites may have consumed compositionally similar diets that were isotopically dissimilar (Fig. 5.5). Although we could not account for herd due to the low number of foraging sites in the DH ($n = 4$), we attempted to account for a latitudinal gradient in $\delta^{15}N_{Fiber}$, in part, by including ecotype in our analyses of diet composition as a correlate of $\delta^{15}N_{Fiber}$. Ecotype, however, was not a significant factor for any forage group (all $P > 0.113$). The $\delta^{15}N_{Fiber}$ (or a similar measure of fecal $\delta^{15}N$) can be used to estimate

$\delta^{15}N$ of the whole diet (Steele and Daniel 1978, Sponheimer et al. 2003, Stewart et al. 2003, Codron and Codron 2009). The $\delta^{15}N$ of fecal material, however, may not reflect the forages consumed when animals move among areas that are isotopically diverse (Stewart et al. 2003, Finstad 2008).

Urinary urea — Similar to whole urine in caribou from northwestern Alaska (approximately -4 to -2‰; Finstad 2008), the $\delta^{15}N_{Urea}$ of wild caribou was generally isotopically "light" ($\bar{x}$ = -4.68‰). For domestic herbivores in positive N balance, the $\delta^{15}N$ of whole urine is also depleted relative to the $\delta^{15}N_{Diet}$. In cattle [*Bos Taurus,* (Linnaeus, 1758); -3.4 to -0.7‰], urine was depleted by 3.7 to 5.3‰ relative to the diet (Sutoh et al. 1987, Knobbe et al. 2006). Similarly, the urine of llamas [*Lama glama* (Linnaeus, 1758); -0.2 to 3.9‰] was also depleted relative to diet but to a smaller degree (-2.1 to -0.3‰; Sponheimer et al. 2003). The $\delta^{15}N_{Urea}$ for caribou and reindeer in captivity (Parker et al. 2005, Barboza and Parker 2006) spanned the range observed in cattle and llamas. For caribou from these 4 herds, there appeared to be no consistent pattern in the depletion of $\delta^{15}N_{Urea}$ relative to $\delta^{15}N_{Diet}$ (Fig. 5.5).

The highly depleted urea in the urine of some of these caribou (e.g., WAH 2007; Fig. 5.5) suggested that urea was derived primarily, if not exclusively, from dietary sources of N. The amount of ^{15}N in urinary urea depends primarily on N flux and the source of N in urea (Parker et al. 2005, Barboza and Parker 2006). Enzymatic preference for ^{14}N during amino acid metabolism (Macko et al. 1986) typically results in the excretion of urea low in $\delta^{15}N$ (Steele and Daniel 1978), although this pattern may vary with the supply of amino acids from catabolized protein. Contributions of body N to the pool of urea N are derived primarily from skeletal muscle (Waterlow 1999, Bell et al. 2000), which is heavier in ^{15}N than dietary proteins (Kelly 2000). Although modified by the formation of ammonia and microbial exchanges of N, inputs to the pool of urea N are primarily through the catabolism of amino acids from forages (Morrison 2000). As catabolism of dietary amino acids and the production of ammonia increase, the $\delta^{15}N$ of the body urea pool begins to reflect that of the diet, and, consequently, isotopically "light" urea is excreted in the urine.

Body proteins — The $\delta^{15}N_{Body}$ among herds and years (2.2 ± 1.56‰, $\bar{x}$ ± SD) was similar to other estimates of $\delta^{15}N_{Body}$ for *Rangifer* spp. (Fig. 5.5), but there were marked inter- and intra-annual differences within each herd (Table 5.4). For caribou in interior and western Alaska, the $\delta^{15}N_{Body}$ (as indexed by red blood cells) ranged from approximately 1.0 to 3.5‰ (Ben-David et al. 2001, Finstad 2008, Adams et al. 2010) which was similar to woodland caribou [*R. t. caribou* (Gmelin, 1788)] in northern British Columbia (2.0 to 2.8‰; Milakovic 2008). Isotopic patterns in $\delta^{15}N_{Body}$ correlate with periods of gain (isotopic depletion) and loss (isotopic enrichment) of the body N pool (Karasov and Martinez del Rio 2007), although these changes in $\delta^{15}N_{Body}$ can be small for large herbivores (Barboza and Parker 2006; 2008). Deposition of body protein primarily occurs in summer, whereas catabolism occurs in late winter through early summer (Gerhart et al. 1996, Chan-McLeod et al. 1999), although anabolism can occur in late winter if caribou have adequate energy reserves and access to high protein forages (Parker et al. 2005, Barboza and Parker 2008). Summer and fall diets high in shrubs (Boertje 1984, Russell et al. 1993) that are low in ^{15}N (Barnett 1994, Finstad 2008) could produce the observed lower estimates of $\delta^{15}N_{Body}$ (e.g., CAH; Fig. 5.5). Alternatively, late summer and fall diets that contain large proportions of enriched forages, such as forbs, graminoids, and mushrooms (Barnett 1994, Finstad 2008), would increase $\delta^{15}N_{Body}$ (e.g., WAH 2006 and 2008; Fig. 5.5). Of course, these predictions are complicated by the nutritional demands of individual caribou that may alter these expected (Ben-David et al. 2001), and admittedly simple, trajectories in enrichment. For example, red blood cells of caribou and reindeer slowly increase in $\delta^{15}N$ during winter as body protein is lost on a low N diet and decline in $\delta^{15}N$ during early lactation as dietary N is incorporated in body protein (Parker et al. 2005, Barboza and Parker 2006). Forage restriction and added demands for energy (e.g., thermoregulation and mobility) or N (e.g., excretion of toxins) may accentuate or ameliorate these patterns of enrichment or depletion (Karasov and Martinez del Rio 2007). Inter- and intra-annual differences among and within years (Table 5.4) reflect the interactions between exogenous inputs throughout the year and the

extent to which caribou may rely on endogenous N to meet the demands of maintenance and reproduction.

Isotopic proxies of protein status

Both metrics of protein status were highly variable between years and among sites (Fig. 5.6). There are inherent limitations to interpreting the *p*-UN for wild caribou. We suggest that the $\Delta_{Body\text{-}urea}$ offers a relative index of protein status that does not require a discrimination factor or an estimate of $\delta^{15}N_{Diet}$, and, correspondingly, we discuss some of the ecological interpretations of our modeling effort.

The proportion of urea N derived from body N (*p*-UN) — Parameters of the isotopic model to estimate *p*-UN were more varied than we expected. The *p*-UN is a proportion that should range from 0 to 1 and deviations from this range suggest that the some parameters of the model may be poorly defined (D. Gustine, unpublished data). We used a simulation model to estimate the *p*-UN in an effort to identify potentially unstable estimates. For some samples ($n = 137$), the simulated estimates of *p*-UN did not fall between 0 and 1 (Fig. 5.6a). The simplest interpretation of these outliers is that they were from animals in either a severe N deficit (*p*-UN > 0.46) or rapid N gain (*p*-UN ≤ 0.46; Barboza and Parker 2006). However, there was both a directional bias and herd effect for the outliers: the *p*-UN for most of these unstable samples was < 0 ($n = 101$) and typically occurred in the WAH ($n = 75$; Fig. 5.6a). As in Gustine et al. (*in press*), we could have used the ranges of simulations and the threshold of 0.46 (Barboza and Parker 2006) to classify samples by N status (positive, maintenance, or negative). However, we are concerned that the factors that affected the *p*-UN in the WAH also may have affected the estimates of *p*-UN in the other herds. We suspect that the actual and potential instability of *p*-UN was due, in part, to the poor temporal resolution of $\delta^{15}N_{Diet}$.

For a vagile ungulate such as caribou that can quickly cross diverse environmental and isotopic gradients, it is possible that there is a temporal mismatch between a fecal measure of $\delta^{15}N_{Diet}$ estimated for a group of caribou at a foraging site and the urea (thereby $\delta^{15}N_{Urea}$) deposited by individual caribou at that site. The pool of urea N in the

body turns over every 9-12 hours (Barboza and Parker 2008), while our measure of $\delta^{15}N_{Diet}$ was derived from fecal samples that represented forages consumed within 50-68 h (Lechner et al. 2010). The urea N derived from diet N may also change quickly between sites as late winter progresses and animals encounter rapidly changing snow conditions and increases in forage availability and possibly quality (Klein 1990, Cebrian et al. 2008). The increased availability of these higher protein forages (e.g., *Carex* and *Eriophorum* spp.; Cebrian et al. 2008) could quickly alter the $\delta^{15}N$ of both the dietary and urea pools, especially if the $\delta^{15}N$ of these forages changes with re-growth. Consequently, the "estimated" $\delta^{15}N_{Diet}$ derived from fecal samples from forages eaten days earlier may not be reflected in the "real" $\delta^{15}N_{Diet}$ (and the associated urea N produced from the "real" diet). We have little evidence, however, of a rapidly changing $\delta^{15}N_{Diet}$: the $\delta^{15}N_{Diet}$ (as indexed from $\delta^{15}N_{Fiber}$ derived from individual fecal samples at each foraging site) was the least variable (SD < 0.72‰) and had the smallest range (-6.40 to -1.50‰) of the isotopes we measured. Additionally, we attempted to time our sampling well before snow ablation and the onset of spring (Table 5.1). For the collections from the WAH in 2007, however, warm weather and rain did remove some of the snowpack, and, consequently, conditions changed rapidly. This collection had the lowest $\delta^{15}N_{Urea}$ and the largest difference between $\delta^{15}N_{Diet}$ and $\delta^{15}N_{Urea}$ of any herd and year (Fig. 5.5). Even though our estimates of $\delta^{15}N_{Body}$ were also lower for these samples, the highly depleted urea N suggested that the pool of urea N was comprised largely of dietary proteins.

We did not observe these complicating factors in applying *p*-UN to populations of semi-captive caribou (Gustine et al., *in press*) and wild muskoxen (D. Gustine, unpublished data). Wild, adult, pregnant caribou that were captured in late winter and kept in a predator exclosure throughout the calving period were given an isotopically distinct diet on an *ad libitum* feeding schedule. Consequently, some of the unidentified sources of variation we recorded in these wild populations of caribou (i.e., sex, age, reproductive status, and temporal resolution of $\delta^{15}N_{Diet}$) were tightly controlled within this semi-captive setting. Similarly, wild muskoxen are very sedentary throughout the winter (Jingfors 1982, Nellemann 1998) and depend heavily on local resources. Thus,

the previously discussed temporal mismatch between the $\delta^{15}N_{Diet}$ and $\delta^{15}N_{Urea}$ that we suspect occurred in wild, free-roaming caribou does not likely occur in muskoxen. Given current technological constraints (e.g., lack of a temporally appropriate measure of $\delta^{15}N_{Diet}$ and the ability to identify reproductive status from a urine-in-snow sample), these factors may prohibit the application of *p*-UN to assess protein status in wild populations of caribou.

Difference between $\delta^{15}N_{Body}$ and $\delta^{15}N_{Urea}$ ($\Delta_{Body\text{-}urea}$) — As indexed by $\Delta_{Body\text{-}urea}$, shrubs constituted a minor but possibly important component in the protein status of caribou. A portion of the observed variance in this index of protein status ($r^2 = 0.26$) among foraging sites was explained by the amount of shrubs in the diet, which was positively related to $\Delta_{Body\text{-}urea}$ in caribou across foraging sites (Fig. 5.7). Shrubs may be an important source of N to diets that are typically lichen-rich and protein-deficient in winter (Storeheier et al. 2002, Parker et al. 2005). Typically, shrubs, especially deciduous shrubs, have been considered minor components of winter diets in both migratory (Russell et al. 1993, Joly et al. 2007) and sedentary caribou (Boertje 1990, Farnell and Gardner 2002). With few exceptions, diets of these groups of caribou were predominately lichens. We recorded a large range in the occurrence of evergreen and deciduous shrubs in the diet for both types of caribou (1-25%; Fig. 5.7), but as others have reported, shrubs typically occurred at low levels ($\bar{x} = 10\%$; Table 5.3). In the winter, shrubs are higher in N (1.0-1.2%) than lichens (0.4%), mosses (0.9%), and graminoids (0.7%) and more digestible (~62%) than forbs (46%), graminoids (54%), and mosses (7%; Boertje 1990). Although the relationship between $\Delta_{Body\text{-}urea}$ and the proportion of shrubs in the diet is linear within the observed range, we suspect that the relationship may be asymptotic or Gaussian if the amount of lichen in the diet decreases with an increase in shrubs. Therefore, an increase in the amount of shrubs in the wintering areas of caribou populations may not be beneficial if shrub expansion is associated with a decrease in lichen biomass (Cornelissen et al. 2001). A decrease in lichens did not result in the increase of a specific forage group within the diets of these groups of caribou (Fig. 5.3).

The interpretation for intermediate values of $\Delta_{Body\text{-}urea}$ remains unclear. As $\delta^{15}N_{Urea}$ approached or exceeded that of $\delta^{15}N_{Body}$ (e.g., sites in CAH 2006 and 2007 and CH 2008; Fig. 5.6b), the pool of urea N in the body was being dominated by endogenous sources and caribou were in negative N balance. Conversely, as the difference between $\delta^{15}N_{Urea}$ and $\delta^{15}N_{Body}$ became large (e.g., WAH and DH in 2007 and 2008; Fig. 5.6b), we are sure that caribou excreted large amounts of dietary N and were in positive N balance (see Fig. 7a in Barboza and Parker 2006). The advantage of $\Delta_{Body\text{-}urea}$ is that it does not require a discrimination factor or an estimate of $\delta^{15}N_{Diet}$ to calculate; thereby it is a much more robust index of protein status than *p*-UN for a highly mobile ungulate such as caribou.

Implications to monitoring protein status

Isotopic monitoring could offer a non-invasive approach to evaluate protein dynamics in wild populations of northern herbivores, but challenges remain in applying the linear-mixing model approach as a tool to monitor populations of highly mobile herbivores. In addition to the previously discussed concerns and inferential problems with random collections of excreta in snow (Saltz et al. 1995, Gustine et al., *in press*), there are additional sampling and analytical constraints. The extent of the variation in the isotopes, particularly $\delta^{15}N_{Urea}$, was unexpected, and this limited our ability to make any inferences at the ecotype and herd levels (Table 5.4). A portion of the observed variance in our index of protein status ($\Delta_{Body\text{-}urea}$) among foraging sites, however, was correlated with the amount of shrubs in the diet. To complicate the high variance we observed in protein status, 190 urine samples could not be used because they were either too low in N to be analyzed or were "lost" during IRMS analysis; this reduced our sample size by 34% (Table 5.1: collected versus analyzed samples of urine). Sample loss was biased by herd and year during a period of warmer and wetter weather (WAH 2007). Therefore, samples with lower N may be diluted by weather that could affect the protein status of caribou and increase bias in a sample set. Future efforts to collect samples of urine in snow should

account for analytical losses of samples and time sample collection well before weather events may dilute samples of urine in snow.

For $\Delta_{Body\text{-}urea}$, it may have been more prudent to expand and focus collections within one large herd (e.g., WAH) or the two smaller herds (CH and DH). For large herds, the value in this approach may to be to compare wintering ranges (e.g., core versus peripheral ranges), habitats (e.g., coastal versus inland physiographies), or foraging conditions (e.g., lichen availability, snow depth, and hardness) among foraging sites within a herd. Acquiring representative samples, however, remains a formidable task for herds that are measured in tens (CAH) or hundreds (WAH) of thousands of animals (Dau 2007, Lenart 2007). Both the *p*-UN and $\Delta_{Body\text{-}urea}$ are better suited for smaller and (or) more sedentary herds of ungulates [e.g., muskoxen (*Ovibos moschatus*, Zimmerman, 1780) or mountain sheep (*Ovis* spp.)]. In addition to addressing most of our concerns detailed above, the logistics and costs of acquiring and analyzing an adequate number of representative samples from smaller herds of more sedentary ungulates to make herd-level inferences would be simpler and lower, respectively.

Until this work, an index of protein status in northern ungulates was lacking. We have presented an approach to monitor protein status with potentially important implications to the resources available for reproduction (Barboza and Parker 2008). Serious challenges remain, however, in applying the linear-mixing model technique (*p*-UN) to caribou across broad scales given current limitations and lack of technologies. Nonetheless, with further refinement, the index of protein status ($\Delta_{Body\text{-}urea}$) may prove useful for evaluating foraging conditions at small spatial scales. Despite the aforementioned challenges, we provided the first comprehensive data set of isotopic values (dietary, urinary urea, and body N, and protein status) and characteristics of foraging sites of a large herbivore across diverse environmental and physiographic gradients. Trends in $\delta^{15}N_{Diet}$ were consistent with winter diets high in lichens and low in ^{15}N. Although our understanding of discrimination factors and protein metabolism remains poor, the $\delta^{15}N_{Urea}$ indicated substantial plasticity in protein metabolism among caribou in late winter. The amount of shrubs in a lichen-rich diet had a positive effect on

$\Delta_{Body\text{-}urea}$ of caribou at foraging sites. Evaluating other sources of variation in $\Delta_{Body\text{-}urea}$, temporal patterns in $\Delta_{Body\text{-}urea}$ throughout winter, as well as the implications of expanding shrub communities in northern systems, remain important areas of research in the nutritional ecology of caribou.

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Table 5.1. The dates of collection, number of foraging sites sampled (analyzed), and sample sizes of excreta collected and analyzed for protein status for 4 caribou herds in Alaska and Yukon Territory, late winter, 2006-2008.

Ecotype	Herd	Year	Date	Foraging sites	Elevation (m)	Slope (°)	Samples	
					$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	Urines	Fecals
Migratory	Central Arctic	2006	12 March-10 April	4 (3)	769 ± 73	16 ± 7.7	60 (32)	65
		2007	14-31 March	5 (3)	957 ± 95	22 ± 3.9	79 (67)	68
		2008	17-18 April	3 (3)	418 ± 114	3 ± 1.9	60 (44)	60
	Western Arctic	2006	7 April	5 (5)	110 ± 5	2 ± 1.5	100 (88)	108
		2007	11-12 April	6 (3)	389 ± 61	21 ± 4.0	90 (21)	100
		2008	9-10 April	3 (3)	95 ± 15	6 ± 3.1	60 (58)	58
Sedentary	Chisana	2006	2 April	6 (5)	1,250 ± 107	7 ± 3.0	29 (19)	30
		2008	28 March	3 (3)	1,146 ± 25	8 ± 3.7	30 (9)	30
	Denali	2007	8-10 March	2 (2)	578 ± 21	3 ± 1.2	30 (25)	30
		2008	22-25 March	2 (2)	678 ± 211	16 ± 12.6	34 (16)	29

Table 5.2. Models used to evaluate the observed variance in 2 isotopic measures of protein status [proportion of urea N derived from body N (p-UN)] and the difference between the isotopic ratio of $^{15}N/^{14}N$ relative to atmospheric N (δ) in body and urea N ($\Delta_{Body\text{-}urea}$)] of caribou ($n$ = 362) at foraging sites (n = 33) in 4 herds from Alaska and Yukon Territory, March and April, 2006-2008.

Isotopic proxy of protein status	Model[a]	r^2	w_i[b]
p-UN	Shrubs[c, d]	0.21	1.00
	PC1 terrain[e]	0.16	0.00
	Diet diversity (H')[f]	0.13	0.00
	PC1 diet[e]	0.09	0.00
	Lichens[c]	0.05	0.00
	Null		0.00
	Mosses[c]	0.00	0.00
	Ecotype	0.00	0.00
$\Delta_{Body\text{-}Urea}$	Shrubs	0.26	1.00
	PC1 terrain	0.19	0.00
	Diet diversity (H')	0.09	0.00
	PC1 diet	0.06	0.00
	Lichens	0.03	0.00
	Null		0.00
	Mosses	0.01	0.00
	Ecotype	0.00	0.00

[a]The number of parameters (K) = 2 for every model except for the null (K = 1).

[b]Akaike weights (Burnham and Anderson 2002).

[c]Proportion of an item in the diets as estimated from microhistology.

[d]The amount of evergreen and deciduous shrubs in the diet.

[e]Loadings from the first (PC1) principal component for correlates of the diet or terrain.

[c]Shannon-Wiener index of diversity (Krebs 1989).

Table 5.3. Composition (percent of diet ± SE) and diversity of diets (H'; Krebs 1989) for groups of caribou by ecotype in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) herds in Alaska and Yukon Territory, late winter, 2006-2008. Composition was estimated by correcting the density of plant fragments in feces for apparent digestibility (Boertje 1990).

Ecotype	Herd	Year	*n*	Lichens	Mosses	Graminoids	Forbs	Evergreen shrubs	Deciduous shrubs	H'
Migratory	CAH	2006	4	76 ± 2.7	9 ± 1.8	6 ± 1.6	1 ± 0.8	3 ± 0.3	4 ± 0.6	1.2 ± 0.10
		2007	4	61 ± 11.7	24 ± 7.5	9 ± 5.7	[a]	3 ± 2.0	4 ± 1.0	1.4 ± 0.16
		2008	3	47 ± 15.3	23 ± 6.5	7 ± 1.6	13 ± 5.3	5 ± 1.9	5 ± 1.3	1.8 ± 0.25
	WAH	2006	5	68 ± 3.5	11 ± 1.6	5 ± 0.8	[a]	7 ± 1.4	8 ± 1.5	1.4 ± 0.09
		2007	6	77 ± 3.0	6 ± 1.3	6 ± 1.0	4 ± 0.7	4 ± 1.1	3 ± 0.7	1.2 ± 0.11
		2008	3	60 ± 4.1	13 ± 2.2	7 ± 1.0	[a]	10 ± 2.3	8 ± 2.2	1.6 ± 0.09
Sedentary	CH	2006	5	72 ± 2.7	13 ± 1.2	1 ± 0.7	4 ± 0.8	5 ± 1.5	5 ± 1.5	1.3 ± 0.10
		2008	3	68 ± 2.8	20 ± 0.2	3 ± 0.7	4 ± 3.4	1 ± 0.3	3 ± 0.2	1.4 ± 0.12
	DH	2007	2	54 ± 6.8	16 ± 0.4	15 ± 2.4	[a]	7 ± 0.5	8 ± 3.4	1.8 ± 0.15
		2008	2	77 ± 5.1	13 ± 0.3	5 ± 3.3	[a]	2 ± 1.4	3 ± 1.4	1.1 ± 0.27

[a]Occurred in less than 0.05% of the diet.

Table 5.4. Main effects of ecotype and herd (as determined from analysis of variance) on primary characteristics of diet and terrain (PC1), isotopic ratios (δ) of N in urinary urea ($\delta^{15}N_{Urea}$), the diet ($\delta^{15}N_{Diet}$), and the body ($\delta^{15}N_{Body}$), the proportion of urea N that is derived from body N (*p*-UN), and the difference between $\delta^{15}N_{Body}$ and $\delta^{15}N_{Urea}$ ($\Delta_{Body\text{-}urea}$) for migratory and sedentary caribou in 4 herds from Alaska and Yukon Territory during late winter, 2006-2008. Effects of herd were nested in year (Year | Herd) and those of site were nested in year (Site | Year).

Dependent variable	*n*	R^2	Ecotype			Herd			Year | Herd			Site | Year		
			df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
PC1 diet[a]	37	0.43	1	7.74	0.109	3	0.27	0.843	6	2.99	**0.023**			
PC1 terrain[a]	39	0.42	1	7.94	0.163	3	0.73	0.570	6	2.40	0.053			
$\delta^{15}N_{Urea}$	465	0.66	1	2.16	0.279	3	0.79	0.540	6	2.63	**0.039**	27	9.21	**<0.001**
$\delta^{15}N_{Diet}$	578	0.78	1	3.19	0.216	3	1.93	0.226	6	0.41	0.865	28	52.93	**<0.001**
$\delta^{15}N_{Body}$[b]	437	0.71	1	0.00	0.957	3	3.29	0.100	6	2.48	**0.048**	27	4.46	**<0.001**
p-UN	379	0.64	1	1.54	0.340	3	1.84	0.241	6	2.95	**0.026**	25	5.71	**<0.001**
$\Delta_{Body\text{-}urea}$	379	0.73	1	0.38	0.601	3	3.43	0.093	6	2.13	0.086	25	7.13	**<0.001**

[a]Loadings from the first principal component (PC1) for characteristics of the diet or terrain.

[b]Estimated from the linear relationship between the $\delta^{15}N$ of red blood cells and the $\delta^{15}N$ of urinary creatinine.

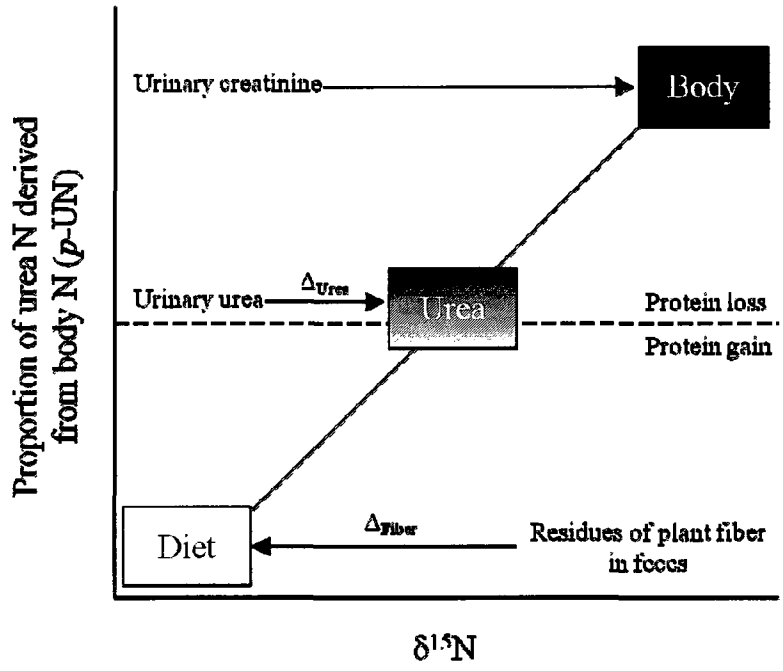

Figure 5.1. A conceptual model for using isotopic ratios of N ($\delta^{15}N$) in excreta to estimate the proportion of urinary urea N that is derived from body N (*p*-UN) to determine N status (as in Gustine et al., *in press*). We derived the relationship between $\delta^{15}N$ of urinary creatinine and body N and discrimination factors [i.e., Δ_{Urea} = depletion of urea from dietary N for animals in positive N balance; Δ_{Fiber} = the enrichment of residues of plant fiber in feces above dietary N] from captive caribou and reindeer.

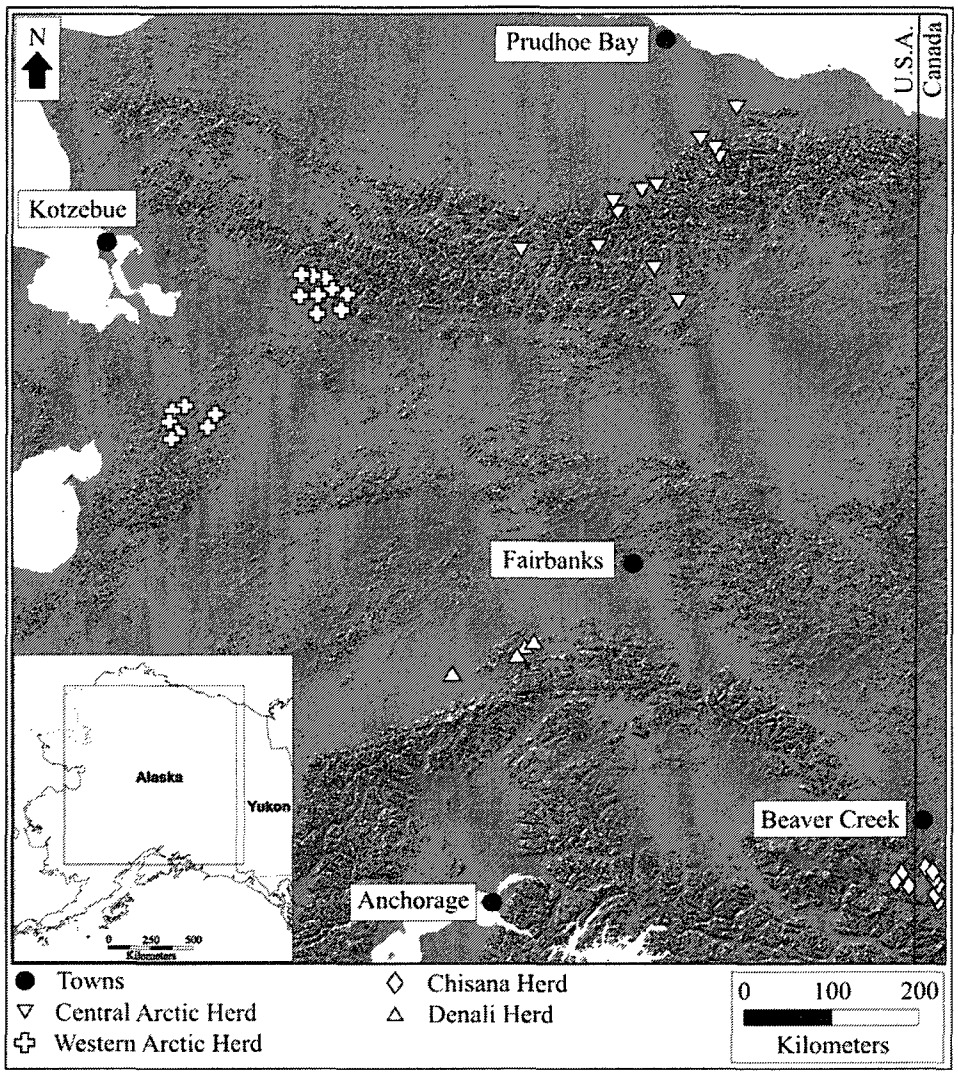

Figure 5.2. Foraging sites (n = 39) of caribou where samples of excreta were collected to estimate the protein status of groups from 4 herds in Alaska and Yukon Territory during late winter, 2006-2008.

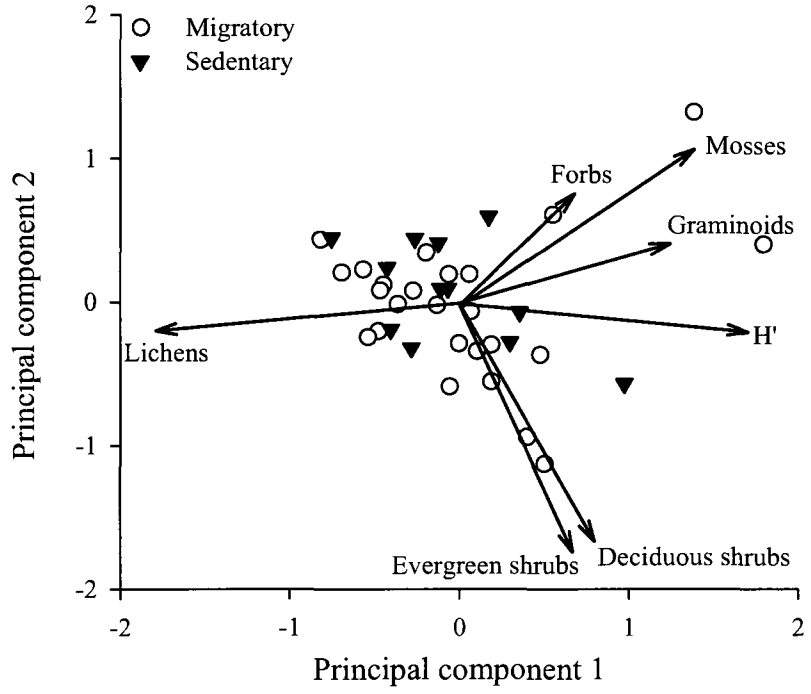

Figure 5.3. Biplot of first and second principal component scores by migratory and sedentary ecotypes of caribou for diet composition and diversity (H'; Krebs 1989) within 4 herds of caribou in Alaska and Yukon Territory during late winter, 2006-2008. Length of lines indicate loadings for each variable.

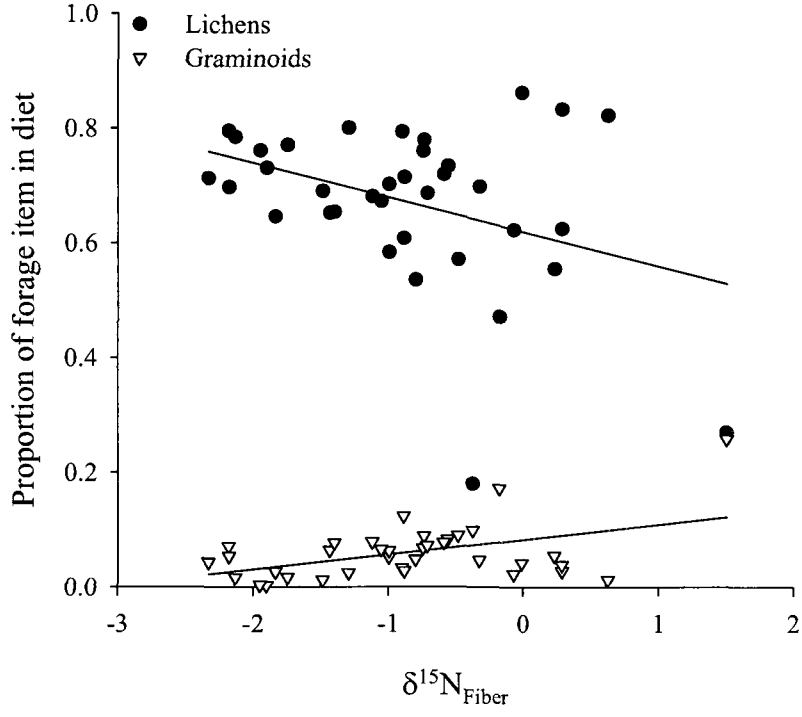

Figure 5.4. Proportions of the lichens and graminoids in the diet in relation to the $\delta^{15}N$ of residues of plant fiber in feces ($\delta^{15}N_{Fiber}$) from 4 caribou herds in Alaska and Yukon Territory during late winter, 2006-2008.

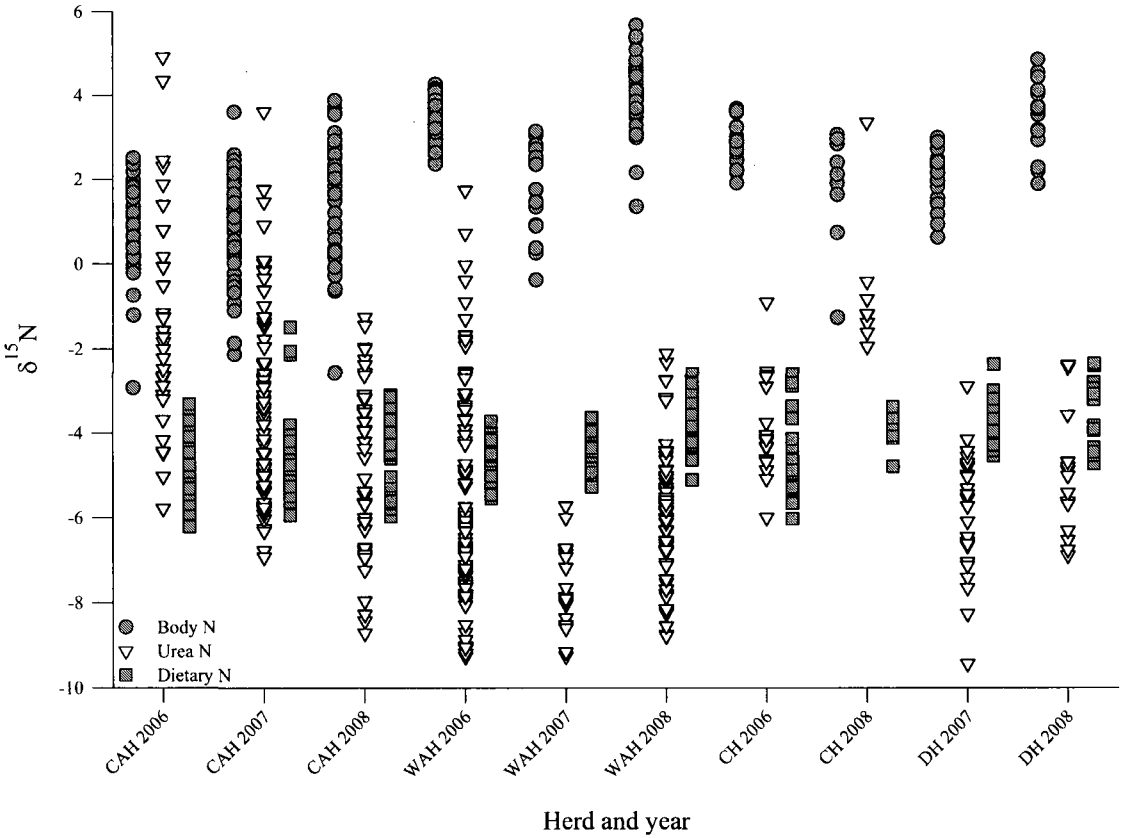

Figure 5.5. The ratios of $^{15}N/^{14}N$ (δ) for body (as derived from urinary creatinine), urinary urea, and dietary N (as estimated from $\delta^{15}N$ of residues of plant fiber in feces) for excreta samples collected from foraging sites within the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds in Alaska and Yukon Territory during late winter, 2006-2008.

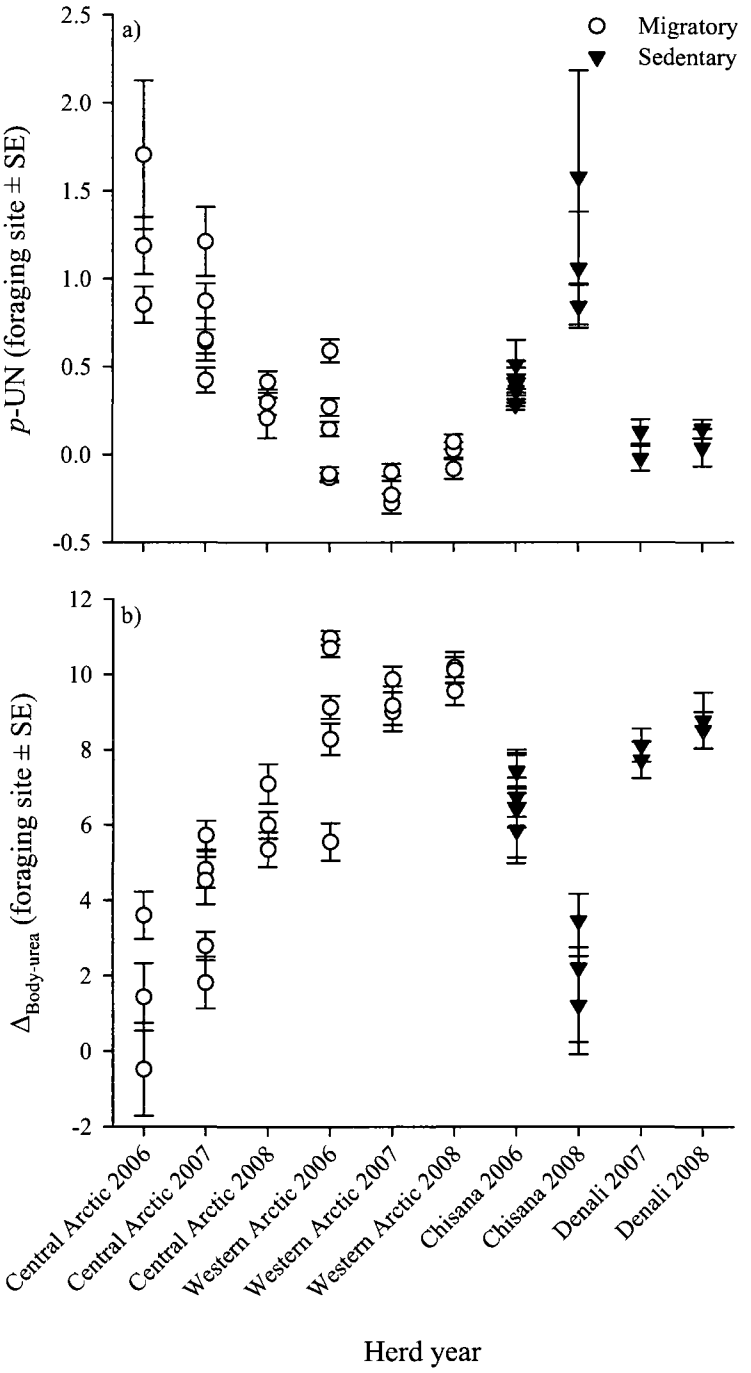

Figure 5.6. The a) proportion of urea N derived from body N (p-UN) and b) the difference between ratios of $^{15}N/^{14}N$ relative to atmospheric N (δ) for body and urea N ($\Delta_{Body\text{-}urea}$) for caribou from 4 herds in Alaska and Yukon Territory during late winter, 2006-2008.

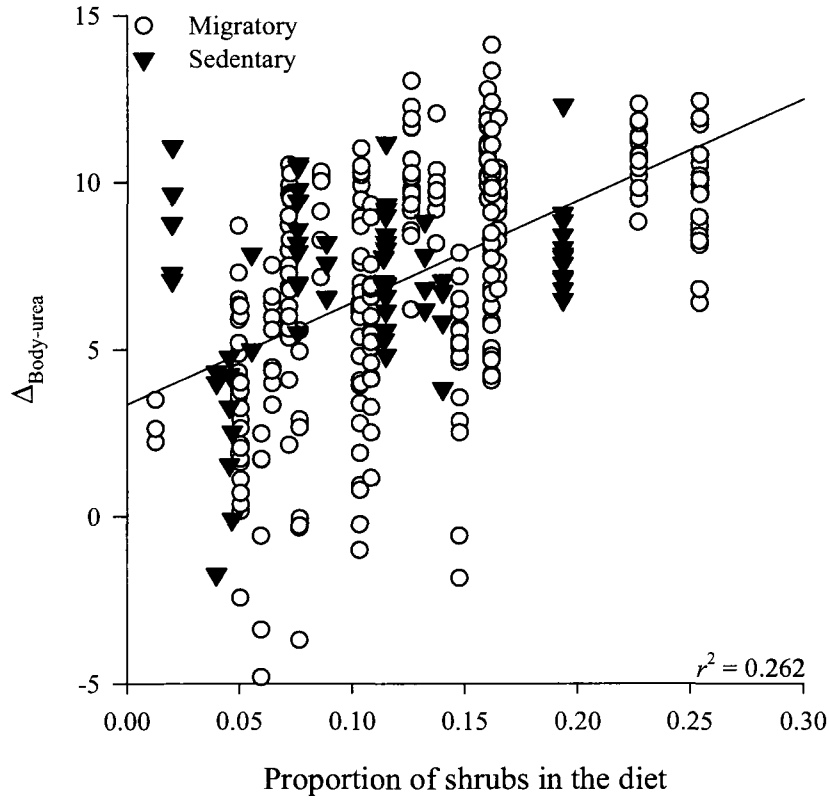

Figure 5.7. The difference between ratios of $^{15}N/^{14}N$ relative to atmospheric N (δ) for body and urea N ($\Delta_{Body\text{-}urea}$) relative to the proportion of shrubs in the diets of caribou at foraging sites (n = 32) from 4 herds in Alaska and Yukon Territory during late winter, 2006-2008.

CHAPTER 6 - CONCLUSIONS

Introduction

The goals of this work were 1) to evaluate and refine the use of a non-invasive, isotopic approach to assess the protein status of wild populations of muskoxen and caribou and 2) to identify characteristics of diet and physiography for wild muskoxen and caribou that have the potential to affect population productivity. I clearly accomplished the first goal, in that I developed and applied techniques to estimate model parameters that were necessary to apply the linear-mixing model set forth in Barboza and Parker (2006) at large-scales. I established important considerations to implement this isotopic approach to monitor the protein status of muskoxen and caribou in late winter, and I provided a candid assessment of the remaining challenges in developing this technique. The second goal was partially addressed: I identified components of diet and physiography for muskoxen and caribou that were correlates of protein status. Although the conceptual link between protein status and population productivity is reasonable, I did not establish causal links between dietary and physiographic associations, protein status, and the productivity of wild populations of muskoxen and caribou. However, to my knowledge, I provided the first associations between components of winter habitats and a proxy of nutritional condition in these northern ungulates.

Muskoxen

In **CHAPTER 2**, I evaluated the protein dynamics of captive female muskoxen by measuring body composition during late gestation, N isotopes in serum and urine, and the birth masses of their calves. In a captive environment under *ad libitum* feeding conditions, all muskoxen lost fat (~24%). Larger, pregnant muskoxen also lost body protein (~6%) throughout late gestation, whereas smaller, non-pregnant females maintained or tended to gain body protein (~6%) in late winter. The pool of serum N was dominated by endogenous proteins, so the proportion of serum amino acids derived from body N (*p*-AN) was not a sensitive metric to assess protein status or strategies of

maternal investment. Unfortunately, due to the lack of snow, I was unable to collect urine samples during Postcalving and this precluded me from fully evaluating *p*-UN in muskoxen. Thus, the precise relationship between N balance and *p*-UN in muskoxen remains undetermined. Therefore, *p*-UN should be considered a relative metric of protein status. Increases in the concentration of plasma urea (Fig. 2.2) and the $\delta^{15}N$ of red blood cells (Fig. 2.4), however, did correspond with losses of body protein which suggested that amino N was oxidized and reutilized between April and Postcalving. Pregnant muskoxen were well within their ability to maintain their tissues by reutilizing amino acids released from mobilized protein. Therefore, reproductive females may have been using dietary N to address the demands of tissue maintenance while stores of body protein were allocated for reproduction (Barboza and Parker 2006, 2008).

The divergent pattern in body protein for reproductive and non-reproductive muskoxen has important ecological implications. As postulated for caribou (Chan-McLeod et al. 1999), the nutritional demands of gestation resulted in a loss of body protein and, given suitable environmental conditions in late winter, a potentially lost "opportunity" to gain body protein. The relationship between the size and availability of body protein as a labile store for reproduction (Fig. 2.3) highlights the importance of summer conditions and lactational status on the capacity of females to reproduce in the variable conditions of arctic and sub-arctic winters (White et al. 1997).

Investment in early reproduction was conservative in muskoxen. Losses of body protein in gestating females were similar to the amount of protein deposited in newborn calves and associated reproductive tissues. Compared to other ungulates (Robbins and Robbins 1979), female muskoxen invest considerably less in their offspring *in utero*. A conservative "strategy" of early reproduction minimizes maternal investment (Stearns 1992) during a period when resource availability is typically declining and uncertain (Gray 1987). The primary reproductive costs are spread throughout an extended period of lactation in muskoxen (Thing et al. 1987, White et al. 1997). Nutrient investment through lactation is highly plastic for reproductive females and this is likely an adaptive response to an inherently variable environment (White and Luick 1984). Variance in

environmental conditions that affect rates of accretion (summer-early winter) and catabolism (winter-spring) of body stores directly affect the availability of body protein as a store for reproduction and the productivity of a population. Consequently, the variance in protein supply from body stores and the diet may explain some of the high variance in reproductive parameters (i.e., pregnancy and calving dates) observed in wild muskoxen.

In **CHAPTER 3**, I presented the first application of an isotopic approach (*p*-UN) to evaluate aspects of winter habitats that affected protein status in groups of wild muskoxen in 3 populations [North Slope(NS), Cape Thompson (CT), and Seward Peninsula (SP)] in northern Alaska from 2005 to 2008. The late winter diets were unexpectedly diverse (as indexed by the Shannon-Wiener Index, Krebs 1989) for a large-bodied grazer. Indeed, diets of muskoxen were more diverse than those of caribou (muskoxen, 1.8 ± 0.08, $\bar{x} \pm 95\%$CI, $n = 33$; caribou, 1.4 ± 0.10, $n = 37$). Diets were dominated either by graminoids and mosses (NS and CT) or lichens and mosses (SP), whereas deciduous shrubs were an important forage group for NS in 2008 (Table 3.3). Similar to Ihl and Klein (2001), lichens accounted for approximately 30% ($n = 24$) of the diet of groups in SP. As proposed for *Rangifer* spp. (Ørskov 1992, Storeheier et al. 2002a), lichens may provide a highly digestible source of carbohydrates that slows catabolism of energy stores while facilitating recycling of urea in muskoxen. The value of lichens as winter forage for muskoxen requires further evaluation, particularly if lichen-tundra associations are to be a casualty of a warmer Arctic (Cornelissen et al. 2001).

Physiography and snow deposition influenced the availability of forage and protein status in muskoxen. The model that corresponded with forage abundance was the most parsimonious explanation of protein status ($R^2 = 0.45$; Table 3.2). Groups of muskoxen at lower elevations with more graminoids in their diets (Schaefer and Messier 1995) relied less on stores of body protein to address their nutritional demands in late winter. Graminoids are often higher in N than many other winter forages (Larter and Nagy 2001b), and, therefore, are an important source of N for reproductive females

during a period when the demands of N for gestation are increasing. Conversely, groups in mountainous areas that were confined to smaller areas (Klein et al. 1993) on less productive ridges (Thing 1984), experienced increased competition for forages, had less graminoids available, and lost body proteins in late winter. Mountainous environments created "islands" of winter habitat for an animal that has little capacity to change foraging areas in winter (Ihl 2007). The interaction of topography, snow deposition, and forage availability emphasizes the spatial distribution of forage resources (Wang et al. 2006) as an important factor in evaluating the quality of winter habitats with implications for the population dynamics of muskoxen (Forchhammer et al. 2002). As noted for red deer (*Cervus elaphus*, Loe et al. 2005, Pettorelli et al. 2005), effects of climate, weather, and topography should be evaluated when predicting the potential impacts of climatic shifts on the population trajectories of muskoxen.

Although components of winter habitats are correlated with the gains or losses of body proteins, the sizes of body protein reserves at the onset of winter may contribute to the resilience of wild muskoxen to variable and (or) severe winter conditions. Changes in the type and timing of precipitation in winter (Walther et al. 2002) are predicted to increase winter severity for northern herbivores (Klein et al. 2005). Losses of body protein in wild muskoxen will decrease the availability of protein stores for reproduction. Due to the sedentary nature of groups of muskoxen, the link between local conditions in winter and protein status is stronger than that of more mobile herbivores. Consequently, the isotopic approach used in this study could be used to assess the reliance of muskoxen on endogenous stores of proteins (i.e., rate of protein loss in late winter). As discussed earlier, there is a relationship between the loss of body protein and the size of the store of body protein in reproductive muskoxen (Fig. 2.3). The sizes of energy and protein stores may contribute to the capacity of muskoxen to endure and recover from foraging constraints in winter (i.e., resilience). Establishment of body stores depends on environmental conditions and reproductive demands during the previous winter and summer (Albon et al. 1987, Gerhart et al. 1997, Cook et al. 2004, McArt et al. 2009). Duration of the period of nutrient gain or replenishment (White 1983), therefore, may be

a critical constraint for muskoxen populations (P. Reynolds, pers. comm.). For example, summer-autumn conditions and associated vegetative productivity on the Seward Peninsula may enable muskoxen to establish substantial body reserves that are used to endure and reproduce in a typically snow-rich winter environment. The Seward Peninsula consistently receives more snowfall (1988-2008 annual difference = 113 ± 33 cm, $\bar{x} \pm$ SD) and more growing degree days than the coastal plain of Alaska (1988-2007 annual difference between the Nome and Kotzebue average and Barrow = 467 ± 102, National Climatic Data Center 2008). Indeed, on Banks Island, summer conditions and diets the year before parturition had a weak but positive relationship with calf production (Larter and Nagy 2001a). Although muskoxen populations may be constrained by a suite of factors (S. Arthur, pers. comm., Gunn and Adamczewski 2003), understanding the relative nutritional contributions of summer and winter conditions to population productivity in muskoxen remains a critical element to conserving and managing populations of muskoxen in a warming Arctic.

Caribou

In **CHAPTER 4**, I assessed isotopic proxies of diet and protein status in a semi-captive population of pregnant caribou in the Chisana Herd (CH) in late winter and identified the potential challenges of population-level assessments of protein status in wild caribou. Females in the exclosure consumed primarily lichens and mosses even though animals were provided a nutritionally complete ration (Fig. 4.2). The $\delta^{15}N$ of residues of plant fiber in feces ($\delta^{15}N_{Fiber}$) tracked the proportion of lichens and ration in their diets (Fig. 4.4). A similar proportion of animals in the exclosure lost core body mass (excluding estimates of fetal and uterine tissues; 55%) and body protein (estimated by *p*-UN; 54%). Pregnant females on *ad libitum* feeding schedules can experience negative N balances in late winter when they mobilize reserves of body protein for the N demands of fetal growth (Barboza and Parker 2008). Similarly, in captive populations of reindeer, animals that experienced identical environmental conditions and were fed the same summer and winter diets exhibited varied nutritional responses during winter

(Barboza and Parker 2006). Wild females from the CH on a formulated ration in a semi-captive environment reflected the diversity in nutritional responses observed in captive caribou and reindeer. However, free-ranging reproductive females in the CH likely experienced more severe protein restrictions during this period.

As noted for muskoxen, the capacity of female caribou to endure late winter conditions and reproduce successfully depends, in a large part, on the interaction of previous reproductive demands (Adams and Dale 1998) and environmental conditions throughout the year that affects the availability of body protein as a labile store for reproduction (Parker et al. 2009). Birth masses of calves are positively correlated with stores of maternal protein (Allaye-Chan 1991), and nutritional restrictions in late winter will constrain the amount of protein available to invest in offspring. Severe winter conditions, that were indexed by snow fall or weather cycles (i.e., Pacific Decadal Oscillation), corresponded with declines in birth masses (Adams 2005) and recruitment of caribou (Hegel et al. 2010). Although this work does not provide a mechanism for the recent decline of the CH (Chisana Caribou Recovery Team 2010), it suggests that we must reexamine the sensitivity of reproductive females to foraging constraints in late winter. The availability of body proteins for reproduction may provide the mechanistic link between environmental conditions, investment in offspring, and population productivity of *Rangifer* spp. (Chan-McLeod et al. 1999, Forchhammer et al. 2002, Tews et al. 2007, Bårdsen 2009).

In **CHAPTER 5**, I presented the first application of isotopic approaches to monitor wild populations of migratory and sedentary caribou in 4 herds (Central Arctic, Western Arctic, Chisana, and Denali) from 2006 to 2008. My objectives were to establish a baseline for monitoring efforts and to identify and discuss elements of winter habitats that may correlate with 2 proxies of protein status in caribou: *p*-UN and $\Delta_{\text{Body-urea}}$. The winter diets of the groups of caribou sampled from these herds were typically dominated by lichens and mosses (>70%) with no differences in diet characteristics between migratory and sedentary ecotypes. As the amount of lichen in the diet decreased, the diversity of the diets increased (Fig. 5.3). Due to substantial intra- and inter-annual variance, isotopes

of N (Fig. 5.5) and protein status (Fig. 5.6) were not different between ecotypes or herds, although some interesting and expected patterns emerged. Urinary urea and dietary N were typically depleted relative to body N ($\delta^{15}N_{Urea}$ = -4.68 ± 2.67‰, $\bar{x}$ ± SD; $\delta^{15}N_{Body}$ = 2.20 ± 1.56‰; $\delta^{15}N_{Diet}$ = -4.18 ± 0.92‰). Dietary and body N of caribou were lighter in ^{15}N than those measured in muskoxen (**CHAPTER 3**: $\delta^{15}N_{Body}$ = 4.74 ± 1.03‰; $\delta^{15}N_{Diet}$ = -2.64 ± 1.17‰), which probably reflects the more depleted diets of caribou through the year. Any potential differences between ecotypes or among caribou herds for isotopes of N and protein status were obscured by the substantial inter- and intra-annual variances within each herd (Fig. 5.5 and 5.6). For our index of protein status ($\Delta_{Body\text{-}urea}$), however, a portion of the observed variance (r^2 = 0.26) could be explained by the proportion of shrubs in the winter diet (Table 5.2). The amount of shrubs in the lichen-rich diets of these caribou had a positive effect on $\Delta_{Body\text{-}urea}$ (Fig. 5.7). As observed in reindeer (Storeheier et al. 2002b), vascular plants, such as shrubs, may form a small but important component of the winter diet that is typically low in N.

Isotopic, analytical, and sampling constraints limit the broad application of the linear-mixing model approach (*p*-UN) to monitoring protein status in caribou. The temporal mismatch between the estimate of $\delta^{15}N_{Diet}$ derived from a fecal proxy ($\delta^{15}N_{Fiber}$) and the turnover time of the urea pool is a source of error for estimation of *p*-UN that is smallest when applied to sedentary herbivores such as muskoxen. The pool of urea N in the body turns over every 9-12 hours (Barboza and Parker 2008), while $\delta^{15}N_{Fiber}$ probably represents forages consumed within 50-68 h (Lechner et al. 2010). Consequently, the "estimated" $\delta^{15}N_{Diet}$ may not match the N in the urea pool especially when animals consume small amounts of winter green forages that are high in N content (Klein 1990).

The discrimination factor for the formation of urea N from dietary N (Δ_{Urea}) may not be fixed for caribou. Linear-mixing models are most sensitive to variance in discrimination factors (Caut et al. 2009, Wolf et al. 2009). I suspect this is part of the reason why the isotopic approach performed well in muskoxen and semi-captive caribou from the CH and poorly in wild caribou. Muskoxen in late winter are very sedentary (Jingfors 1982, Nellemann 1998) and are highly dependent on resource availability at

very small scales. Similarly, penned females in the CH were on an *ad libitum* feeding schedule with very little variance in forage availability. Wild caribou, however, likely experienced episodic periods of diverse forage availability and foraging bouts (Maier and White 1998) and this may have affected Δ_{Urea}, which is the most sensitive parameter of the linear-mixing model that estimates *p*-UN (D. Gustine, unpublished data). Variance in Δ_{Urea} could be due to periods of fasting and re-feeding that may affect N status at small temporal scales, and consequently, the shuttling of N among circulating pools of N within the body (P. Barboza, J. Addison, and D. Gustine, unpublished data).

I suspect that the influence of urea recycling on the isotopic composition of the body urea pool of N may be negligible, although the effect of urea recycling in ruminants to the isotopic composition of the body pool of urea N remains poorly understood (see review in Kelly 2000). The size of the pool of urea N does not change with intake (Van Soest 1994), but the proportion of recycled urea N that enters the body pool of urea N increases as food intakes decline (Barboza et al. 2009). The amount of N from recycled urea, however, is small when compared with the flow of N from amino acids released by protein turnover (Barboza and Parker 2006). Thus, the $\delta^{15}N$ of urinary urea remains representative of the isotopic composition of the body pool of urea N, which is derived from both endogenous (body) and exogenous (diet) N.

Loss of samples and the observed variance in isotopes of N in wild populations accentuate the need to collect large numbers of urine samples from each group or population. The dilution of N metabolites in urine by snow and the loss of samples to IRMS analysis could easily exceed 20% (12-34%; muskoxen and caribou). When these reductions in sample sizes are coupled with the diversity I observed in N isotopes (especially for wild caribou) the capacity to detect any potential differences between or among populations is limited. Consequently, the ability to acquire a representative number of samples from a large, migratory population of caribou becomes exceedingly difficult without a substantial commitment of resources. An index of protein status that does not require a discrimination factor or an estimate of $\delta^{15}N_{Diet}$ (e.g., $\Delta_{Body\text{-}urea}$), however, could be a valuable monitoring tool for assessing relationships between

characteristics of wintering habitats, protein status, and population productivity in smaller, more sedentary populations of caribou (e.g., CH, DH).

In spite of these challenges, I gained valuable new insights into the nutritional and isotopic ecology of caribou. I reported the first paired data set of characteristics of foraging sites and isotopic values (dietary, urinary urea, and body N, and protein status) of a large herbivore. Other sources of variation in $\Delta_{Body\text{-}urea}$ (e.g., reproductive status), temporal patterns in $\Delta_{Body\text{-}urea}$ throughout winter, as well as the implications of expanding shrub communities in northern systems remain important areas of research in the nutritional ecology of caribou. With appropriate considerations and further refinement, the application of an isotopic monitoring program could be an important component of long-term inventory and monitoring programs of other northern herbivores.

Candidate Species for Isotopic Monitoring

There is growing interest in applying this approach to other northern ungulates. The applicability and value of this isotopic technique to monitor protein status in other ungulates depends primarily on the following: 1) the capacity of the isotopic technique to be validated in a captive setting; 2) the ability to acquire a large number of excreta samples in late winter in vegetative associations and snow conditions that are amenable to survey efforts; and 3) life-history characteristics (diets and seasonal movements) that minimize sources of variation within the estimates of model parameters (if using *p*-UN) and attenuate the relationship between local resource and environmental characteristics and annual reproduction (e.g., reduced seasonal movements). In Alaska, mountain sheep (*Ovis* spp.) and bison (*Bison bison*) may meet all these criteria for application. Sheep and bison persist in moderate to large groups at reasonable concentrations during winter in open habitats that are usually covered with snow. Sheep and bison have simpler diets (graminoids and forbs) than do moose. Although there are exceptions (bison, T. Hegel, pers. comm.), all 3 species typically have localized extents of seasonal movements in late winter (Meagher 1986, Walker et al. 2007, Gillingham and Parker 2008). The primary constraint on applying these isotopic approaches to moose are their typically solitary

behavior in vegetative associations with tall shrubs or timber, which would increase the amount of effort per sample collected.

Regardless of the species of interest, investigators should also consider the spatio-temporal extent of their sampling efforts and the simultaneous acquisition of locational and demographic data. Members of a population at the edge of the distribution are most susceptible to environmental and ecological limitations that may impair their ability to acquire resources to reproduce (Caughley and Sinclair 1994). Consequently, trends in protein status of peripheral members of the population are likely not indicative of the population as a whole. Therefore, locational data are necessary to direct sampling efforts to the core of a population's distribution, unless comparing the protein status among ranges (e.g., core versus peripheral ranges) is of interest. Additionally, basic demographic data on population size, age and sex structure, and productivity through spring and late winter would complement any sample design to assess protein status as well as offer valuable context behind the relationships between protein status and population productivity. However, until individuals and their offspring can be identified repeatedly from collections of urine in snow, the causal links between protein status in late winter, parameters of individual fitness, and population productivity will remain elusive.

Invasive Alternatives to Estimating Protein Status

Although non-invasive approaches may be the only way to monitor populations of northern ungulates in conservation units or in some locales, more invasive tools have the potential to establish causal relationships between protein status in late winter, reproductive success and fitness, and population productivity. An isotopic measure of protein status can be determined from blood samples. The $\delta^{15}N$ in serum proteins and amino acids and red blood cells can be used to estimate the relative contributions of endogenous and exogenous proteins to the pool of circulating proteins and amino acids (P. Barboza, D. Gustine, and J. Addison, unpublished data). By targeting adult females through routine collaring efforts, researchers could develop long-term profiles of the

protein dynamics, space use, and foraging constraints of individuals in populations and their offspring. As such, they would establish important mechanistic links between intra- and inter-annual variance in environmental conditions, the use and selection of vegetative associations at multiple scales, nutritional trajectories, the production and survival of offspring, and, ultimately, life-history trade-offs that may affect fitness. The advantages of invasive versus non-invasive measures depend on research questions, resources, and settings.

Implications

Until now, researchers and managers have not been able to non-invasively monitor protein status in northern ungulates. Clearly challenges remain, but despite the aforementioned constraints, this work has provided the following valuable insights into the nutritional and isotopic ecology of muskoxen and caribou. Regardless of environmental conditions in late winter, pregnant muskoxen (**CHAPTER 2**) and caribou (**CHAPTER 4**) are obligated to invest body proteins into offspring. The availability of body protein as a labile reserve for reproduction depends, in part, on environmental conditions that affect rates of accretion (summer-autumn) and depletion of body stores (winter-late winter). The non-invasive isotopic model of protein status seems well suited to evaluate linkages between habitat characteristics and protein status (*p*-UN) in late winter for sedentary herbivores. Muskoxen are highly dependent on the localized availability of forage resources in winter, and, consequently, the link between characteristics of foraging sites and protein status of groups of muskox was stronger than for caribou. Interactions of physiography and snow deposition that limit the abundance of graminoids and influx of dietary N in late winter increase the reliance of groups of muskoxen on their body proteins to address their nutritional requirements (**CHAPTER 3**). Alternatively, caribou are well adapted to surviving and reproducing on forages that persist across larger, more variable environments than muskoxen. The ability of caribou to respond to changes in forage availability through movement presented challenges in estimating parameters of the model to estimate *p*-UN and weakened the link between

characteristics of foraging sites and our index of protein status ($\Delta_{Body\text{-}urea}$). As noted by Storeheier et al. (2002b), vascular plants (in this case deciduous and evergreen shrubs) may comprise a small but important component of the winter diet that minimizes the reliance of caribou on stores of body protein (**CHAPTER 5**). An approach that identifies reproductive females within a sample (e.g., a blood-based measure) would be a more sensitive metric of protein status and, thereby, provide a potential causal link to changes in population productivity. The success of an isotopic monitoring approach for the conservation and management of northern ungulates will depend on further development and validation.

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APPENDICES

Appendix A. Body composition and isotopes of N in captive female muskoxen during winter

Table A.1. Body composition of captive female muskoxen by reproductive status, Fairbanks, Alaska, 2007 (pgs. 172-174).

Animal	Date	Age (y)	Reproductive status	Body composition				
				Body mass (kg)	Lean mass[a] (kg)	Body protein[b] (kg)	Total fat[a] (kg)	Depth of rump fat[c] (cm)
8	7-Feb-07	13	Not pregnant	256.0	123.3	25.5	67.7	5.40
65	7-Feb-07	19	Not pregnant	202.5	107.3	22.2	43.8	2.40
138	7-Feb-07	15	Not pregnant	228.5	101.0	20.9	69.5	2.90
140	7-Feb-07	15	Not pregnant	189.0	110.9	23.0	30.1	2.00
165	7-Feb-07	17	Not pregnant	202.0	118.3	24.5	32.5	2.00
183	7-Feb-07	11	Not pregnant	265.0	116.8	24.2	81.0	5.80
184	7-Feb-07	11	Not pregnant	242.0	99.0	20.5	81.6	4.40
195	7-Feb-07	10	Pregnant	257.0	119.9	24.8	71.9	4.90
196	7-Feb-07	10	Pregnant	274.0	129.2	26.7	75.3	4.40
200	7-Feb-07	10	Not pregnant	246.5	115.6	23.9	68.3	4.30
221[d]	7-Feb-07	4	Pregnant	223.0				2.00
223	7-Feb-07	3	Pregnant	215.5	130.5	27.0	30.3	2.60
931	7-Feb-07	12	Not pregnant	212.5	99.8	20.7	58.8	3.60
952	7-Feb-07	8	Pregnant	239.0	120.9	25.0	57.5	4.60
958	7-Feb-07	8	Pregnant	244.0	110.1	22.8	72.0	3.30
8	7-Mar-07	13	Not pregnant	259.0				5.00
65	7-Mar-07	19	Not pregnant	199.0				3.10
138	7-Mar-07	15	Not pregnant	225.0				2.80
140	7-Mar-07	15	Not pregnant	190.0				1.60
165	7-Mar-07	17	Not pregnant	202.0				2.00
183	7-Mar-07	11	Not pregnant	265.0				6.00
184	7-Mar-07	11	Not pregnant	240.0				4.20
195	7-Mar-07	10	Pregnant	258.0				5.20

Table A.1. Body composition of captive female muskoxen by reproductive status, Fairbanks, Alaska, 2007 (pgs. 172-174).

Animal	Date	Age (y)	Reproductive status	Body composition				
				Body mass (kg)	Lean mass[a] (kg)	Body protein[b] (kg)	Total fat[a] (kg)	Depth of rump fat[c] (cm)
196	7-Mar-07	10	Pregnant	274.0				4.40
200	7-Mar-07	10	Not pregnant	245.5				3.60
221	7-Mar-07	4	Pregnant	219.5				2.00
223	7-Mar-07	3	Pregnant	217.5				2.70
931	7-Mar-07	12	Not pregnant	212.5				3.70
952	7-Mar-07	8	Pregnant	247.0				4.30
958	7-Mar-07	8	Pregnant	248.5				3.60
8	4-Apr-07	13	Not pregnant	255.0				3.90
65	4-Apr-07	19	Not pregnant	198.0				2.00
138	4-Apr-07	15	Not pregnant	223.5				3.40
140	4-Apr-07	15	Not pregnant	189.0				1.70
165	4-Apr-07	17	Not pregnant	201.5				2.10
183	4-Apr-07	11	Not pregnant	265.0				5.80
184	4-Apr-07	11	Not pregnant	242.5				4.80
195	4-Apr-07	10	Pregnant	255.0				5.00
196	4-Apr-07	10	Pregnant	269.0				5.10
200	4-Apr-07	10	Not pregnant	247.0				3.30
221	4-Apr-07	4	Pregnant	217.0				2.40
223	4-Apr-07	3	Pregnant	214.5				2.70
931	4-Apr-07	12	Not pregnant	216.5				3.70
952	4-Apr-07	8	Pregnant	247.0				4.60
958	4-Apr-07	8	Pregnant	247.0				3.10
8	5-May-07	13	Not pregnant	249.0	131.2	27.2	54.6	4.00

Table A.1. Body composition of captive female muskoxen by reproductive status, Fairbanks, Alaska, 2007 (pgs. 172-174).

Animal	Date	Age (y)	Reproductive status	Body composition				
				Body mass (kg)	Lean mass[a] (kg)	Body protein[b] (kg)	Total fat[a] (kg)	Depth of rump fat[c] (cm)
65	11-Jun-07	19	Not pregnant	192.5	97.9	20.3	45.8	1.30
138	2-Jul-07	15	Not pregnant	220.5	134.6	27.9	30.0	3.20
140	8-May-07	15	Not pregnant	177.0	123.8	25.6	8.3	1.10
165	2-Jul-07	17	Not pregnant	191.5	111.9	23.2	31.0	1.90
183	7-May-07	11	Not pregnant	258.0	113.4	23.5	79.2	5.50
184	11-Jun-07	11	Not pregnant	226.0	115.9	24.0	52.8	4.00
195	5-May-07	10	Pregnant	234.5	113.5	23.5	61.5	3.30
196	7-May-07	10	Pregnant	243.5	121.4	25.1	60.3	3.10
200	11-Jun-07	10	Not pregnant	232.5	119.4	24.7	54.5	3.10
221[e]	7-May-07	4	Pregnant	187.5				1.80
223	8-May-07	3	Pregnant	190.0	122.3	25.3	19.5	1.60
931	7-May-07	12	Not pregnant	177.0	100.9	20.9	52.8	2.40
952[e]	11-Jun-07	8	Pregnant	217.0	105.2	21.8	56.8	3.10
958[e]	28-May-07	8	Pregnant	200.0	110.1	22.8	39.2	2.50

[a]Estimated by dilution of body water with tritiated water.

[b]Estimated as in Adamczewski [1995; body protein (kg) = 0.207 × lean mass (kg)].

[c]Measured by ultrasonography (e.g., Rombach et al. 2003).

[d]Not included in analyses because she was not a tractable animal.

[e]Calf died.

Table A.2. Isotopes of N ($\delta^{15}N$) in samples from captive female muskoxen, Fairbanks, Alaska, 2007 (pgs. 175-177).

Animal	Date	$\delta^{15}N$						
		Urea	Creatinine	Red blood cells	Fiber[a]	Serum amino acids	Serum urea	Serum proteins
8	7-Feb-07	-1.535	0.074	5.083	3.655	4.807	4.096	6.536
65	7-Feb-07	0.367	0.373	5.881	4.844	2.267	5.032	5.727
138	7-Feb-07	-0.860	0.195	5.370	4.137	2.747	7.052	6.036
140	7-Feb-07	-0.466	0.272	6.506	4.381	2.529	5.262	5.543
165	7-Feb-07	-0.430	0.292	6.204	4.639	3.281	5.846	5.726
183	7-Feb-07	-1.739	0.029	5.636	3.872	3.961	5.447	5.840
184	7-Feb-07	-0.794	0.227	5.805	3.521	3.800	4.472	5.688
195	7-Feb-07	-0.591	0.261	5.724	3.673	3.632	4.892	5.201
196	7-Feb-07	-2.094	-0.049	5.984	4.366	3.887	5.170	4.892
200	7-Feb-07	-0.520	0.286	6.205	3.908	3.854	5.513	5.981
221	7-Feb-07	-2.352	-0.102		3.585			
223	7-Feb-07	-2.490	-0.135	6.070	3.078	2.010	6.113	5.734
931	7-Feb-07	-2.201	-0.066	4.743	3.507	1.523	8.690	4.932
952	7-Feb-07	-1.490	0.076	5.203	3.428			4.645
958	7-Feb-07	-2.217	-0.075	5.251	3.444	3.953	8.763	5.250
8	7-Mar-07	-1.393	0.160	5.279	3.347			5.974
65	7-Mar-07	-0.820	0.245	5.548	3.160			5.028
138	7-Mar-07	-0.986	0.222	5.746	4.114			5.488
140	7-Mar-07	-0.523	0.286	5.619	4.251			5.072
165	7-Mar-07	-1.700	0.099	5.787	3.997			6.128
183	7-Mar-07	-0.799	0.288	5.316	3.676			5.892
184	7-Mar-07	-0.361	0.335	5.578	3.350			5.821
195	7-Mar-07	-1.586	0.126	5.030	3.295			5.460
196	7-Mar-07	-1.217	0.200	5.637	4.042			5.283

Table A.2. Isotopes of N ($\delta^{15}N$) in samples from captive female muskoxen, Fairbanks, Alaska, 2007 (pgs. 175-177).

Animal	Date	$\delta^{15}N$						
		Urea	Creatinine	Red blood cells	Fiber[a]	Serum amino acids	Serum urea	Serum proteins
200	7-Mar-07	-2.586	-0.068	5.710	3.711			5.202
221	7-Mar-07	-1.020	0.209		3.050			
223	7-Mar-07	-1.252	0.205	4.874	2.903			4.489
931	7-Mar-07	-1.029	0.216	5.060	3.866			5.179
952	7-Mar-07	-2.276	-0.005	4.775	3.380			4.840
958	7-Mar-07	-0.998	0.250	4.765	3.031			4.578
8	4-Apr-07	-0.916	0.270	5.383	2.847			
65	4-Apr-07	-0.149	0.369	5.510	4.662			
138	4-Apr-07	0.000	0.432	5.656	3.235			
140	4-Apr-07	-0.988	0.234	6.090	3.547			
165	4-Apr-07	-0.637	0.302	5.152	3.151			
183	4-Apr-07	0.198	0.719	5.500	3.069			
184	4-Apr-07	0.420	0.586	5.617	2.942			
195	4-Apr-07	-0.093	0.421	5.412	2.817			
196	4-Apr-07	-2.167	0.025	5.333	3.803			
200	4-Apr-07	-2.019	0.053	5.876	3.786			
221	4-Apr-07	-3.166	-0.135		2.611			
223	4-Apr-07	-1.210	0.230	4.192	2.873			
931	4-Apr-07	-1.442	0.173	4.723	3.083			
952	4-Apr-07	-0.740	0.308	4.227	2.551			
958	4-Apr-07	-1.525	0.166	4.438	2.958			
8	5-May-07			5.151		5.209	6.397	6.492
65	11-Jun-07			4.961		5.008	9.105	6.319
138	2-Jul-07			5.097		4.876	6.021	5.828

Table A.2. Isotopes of N ($\delta^{15}N$) in samples from captive female muskoxen, Fairbanks, Alaska, 2007 (pgs. 175-177).

Animal	Date	$\delta^{15}N$						
		Urea	Creatinine	Red blood cells	Fiber[a]	Serum amino acids	Serum urea	Serum proteins
140	8-May-07			5.447		4.007	5.604	5.245
165	2-Jul-07			5.255		4.668	5.720	5.798
183	7-May-07			5.379		3.077	7.156	6.726
184	11-Jun-07					2.890	8.207	
195	5-May-07			5.256		5.240	10.158	5.118
196	7-May-07			5.522		2.524	7.897	5.415
200	11-Jun-07			5.556		3.404	7.982	6.600
221	7-May-07							
223	8-May-07			5.133		4.122	10.154	6.142
931	7-May-07			5.371		2.975	6.559	5.898
952	11-Jun-07			5.967				5.953
958	28-May-07			6.187		3.167	6.035	6.229

[a]Estimated from the $\delta^{15}N$ of residues of plant fibers in feces that were rinsed with boiling water.

Appendix B. The relationship between isotopic ratios of N in urinary creatinine and red blood cells in northern ungulates

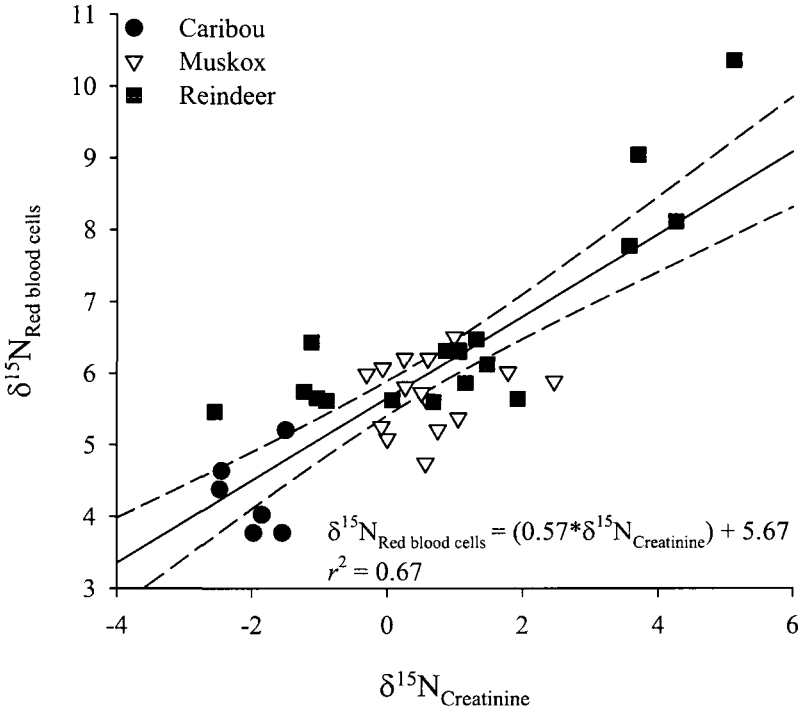

Figure B.1. The relationship between the isotopic ratio of $^{15}N/^{14}N$ (δ) in muscle (caribou) or red blood cells (muskoxen and reindeer) and urinary creatinine in wild caribou (northern Quebec) and captive muskoxen and reindeer (Fairbanks, AK), 2003-2007. Dashed lines denote the 95% confidence interval of the relationship.

Appendix C. A simulation model to estimate the proportion of urea N derived from body N in northern ungulates

Table C.1. Definitions of terms in the schematic for the structure of the simulation model (see Fig. C.1) that was used to define a median and a plausible range of solutions for the linear-mixing model for estimating the proportion of urea N derived from body N in muskoxen and caribou, 2005-2008.

Parameter	Definition
$\delta^{15}N_{Fiber}$	The isotopic ratio of N relative to atmospheric N in the residues of plant fibers in feces.
$E_{Isotope}$	The error associated with estimating each $\delta^{15}N$ via isotopic ratio mass spectrometer (as estimated from the error associated with measuring $\delta^{15}N$ of peptone, n = 149, 0.39‰).
$\delta^{15}N_{SIM.\ Fiber}$	The simulated estimate of $\delta^{15}N_{Fiber}$ for one iteration of the simulation model.
Δ_{Fiber}	The discrimination factor used to correct for fractionation of ^{14}N in the consumption and defecation of forages ($\delta^{15}N_{Fiber}$ of captive animals - $\delta^{15}N_{Diet}$ of captive animals = Δ_{Fiber}; muskoxen, n = 14, 2.82 ± 0.50‰, $\bar{x}$ ± SD; caribou, n = 26, 3.34 ± 1.17‰).
$\Delta_{SIM.\ Fiber}$	The simulated estimate of Δ_{Fiber} for one iteration of the simulation model.
$\delta^{15}N_{SIM.\ Diet}$	The simulated estimate of $\delta^{15}N_{Diet}$ for one iteration of the simulation model.
Δ_{Urea}	The discrimination factor used to correct for fractionation of ^{14}N in the initial creation of urea N from dietary N in the body-urea pool of N ($\delta^{15}N_{Diet}$ of captive animals - $\delta^{15}N_{Urea}$ of captive animals in positive N balance = Δ_{Urea}; muskoxen, n = 6, 2.9 ± 0.78‰, $\bar{x}$ ± SD; caribou, n = 15, 2.35 ± 0.89‰).
$\Delta_{SIM.\ Urea}$	The simulated estimate of Δ_{Urea} for one iteration of the simulation model.
$\delta^{15}N_{Urea}$	The isotopic ratio of N relative to atmospheric N in urinary urea.
$\delta^{15}N_{SIM.\ Urea}$	The simulated estimate of $\delta^{15}N_{Urea}$ for one iteration of the simulation model.
$\delta^{15}N_{Creatinine}$	The isotopic ratio of N relative to atmospheric N in urinary creatinine.
$\Delta_{SIM.\ Creatinine}$	The simulated estimate of $\delta^{15}N_{Creatinine}$ for one iteration of the simulation model.
$\delta^{15}N_{RBC}$	The isotopic ratio of N relative to atmospheric N in red blood cells.
SIM. m	The simulated estimate of slope of the linear regression of $\delta^{15}N_{RBC}$ on $\delta^{15}N_{Creatinine}$ for one iteration of the simulation model.
SIM. b	The simulated estimate of intercept of the linear regression of $\delta^{15}N_{RBC}$ on $\delta^{15}N_{Creatinine}$ for one iteration of the simulation model.
$\delta^{15}N_{SIM.\ Body}$	The simulated estimate of $\delta^{15}N_{Body}$ for one iteration of the simulation model.

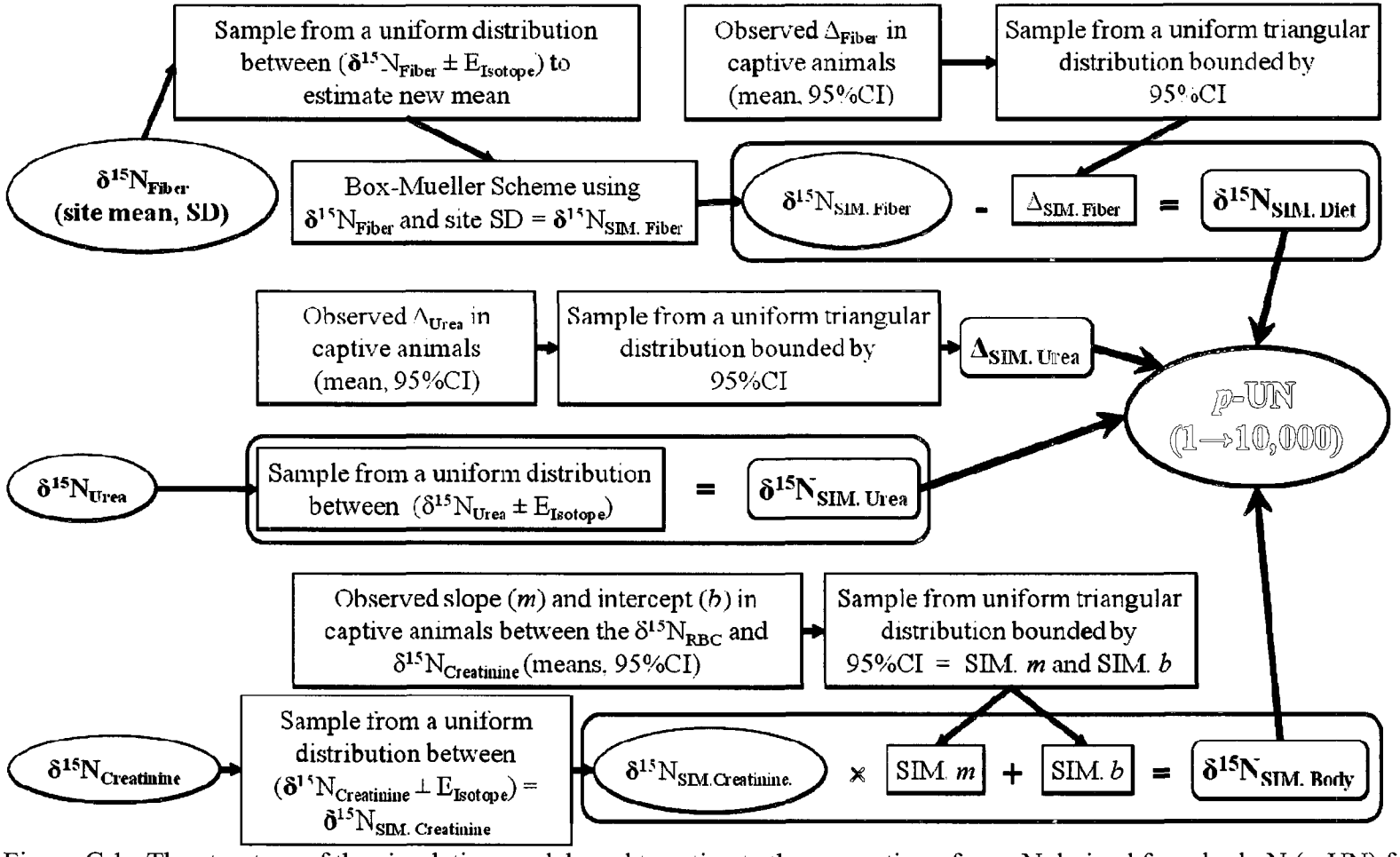

Figure C.1. The structure of the simulation model used to estimate the proportion of urea N derived from body N (p-UN) from isotopes of N in the excreta ($\delta^{15}N_{Fiber}$, $\delta^{15}N_{Urea}$, and $\delta^{15}N_{Creatinine}$) of muskoxen and caribou, 2005-2008.

Appendix D. Foraging sites, microhistology, and isotopes of N in the excreta of wild muskoxen in late winter

Table D.1. The locations and physiographic features of the sites used by groups of muskoxen in 3 populations [North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP)] in northern Alaska, late winter, 2005-2008 (pgs. 184-185).

Population	Year	Site no.	Coordinates[a]		Elevation (m)	Slope (°)	Group size and composition[b]			
			Latitude (N)	Longitude (W)			Size	Adults	Adult females	Yearlings
NS	2007	32	68.7958	148.7267	518.2	3.7	42	0.56	0.56	0.03
NS	2007	33	70.4522	149.1249	4.9	0.0	47	0.64	0.44	0.05
NS	2007	34	70.2227	148.3179	14.0	0.3	43	0.48	0.40	0.12
NS	2008	35	70.4855	149.2201	7.9	0.8	43	0.49	0.37	0.07
NS	2008	36	70.2030	148.2828	14.0	0.7	48	0.38	0.27	0.09
NS	2008	37	69.7006	148.5380	138.1	0.0	38	0.71	0.53	0.00
CT	2007	38	67.1616	163.5561	182.0	18.1	31			0.19
CT	2007	39	67.1558	163.0528	192.0	39.0	25			0.16
CT	2007	40	67.2217	163.6609	96.0	9.7	19			
SP	2005	1	66.2775	163.8701	13.1	0.0	16	0.56	0.44	0.06
SP	2005	2	65.7113	165.4231	440.4	10.8	16	0.63	0.44	0.00
SP	2005	3	65.8047	165.3975	148.1	13.8	15	0.33	0.20	0.20
SP	2005	5	65.9094	165.6814	131.1	15.0	14	0.71	0.64	0.00
SP	2005	6	65.9590	166.2274	308.5	26.0	15	0.47	0.33	0.13
SP	2005	7	65.9253	166.2764	362.1	48.4	50	0.40	0.32	0.18
SP	2005	8	65.5025	167.6717	79.9	36.6	8	0.38	0.38	0.13
SP	2005	9	65.5743	167.4609	381.9	19.5	17	0.29	0.24	0.24
SP	2005	10	65.6529	167.4948	197.8	10.5	10	0.90	0.30	0.00
SP	2005	11	65.6599	167.5602	322.5	4.4	31	0.29	0.26	0.19
SP	2005	12	65.6508	167.5523	278.3	3.5	26	0.38	0.31	0.31
SP	2006	13	65.5871	164.2999	305.4	9.2	30	0.40	0.40	0.07
SP	2006	14	65.4104	165.3474	336.8	8.5	34	0.44	0.44	0.09
SP	2006	15	65.1914	164.4736	90.8	12.4	20	0.40	0.40	0.15
SP	2006	16	65.8310	165.5710	253.3	11.3	20			

Table D.1. The locations and physiographic features of the sites used by groups of muskoxen in 3 populations [North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP)] in northern Alaska, late winter, 2005-2008 (pgs. 184-185).

Population	Year	Site no.	Coordinates[a]		Elevation (m)	Slope (°)	Group size and composition[b]			
			Latitude (N)	Longitude (W)			Size	Adults	Adult females	Yearlings
SP	2006	17	65.5508	165.5710	443.8	14.5	16			
SP	2006	18	65.5029	165.3254	346.6	4.0	33	0.70	0.58	0.09
SP	2006	19	65.4521	166.7375	83.5	12.9	36	0.58	0.47	0.17
SP	2007	20	64.5789	165.7772	149.4	22.8	52	0.62	0.62	0.17
SP	2007	21	64.6299	165.1083	70.0	7.1	20	0.50	0.40	0.05
SP	2007	22	64.7353	166.2171	169.2	6.6	19	0.79	0.32	0.16
SP	2007	23	64.6828	166.2861	103.6	33.3	20	0.75	0.70	0.00
SP	2007	24	64.6610	165.2499	513.3	58.6				
SP	2008	25	64.5597	165.3865	256.3	36.4	23	0.57	0.43	0.17
SP	2008	26	64.5941	165.0750	239.6	8.1	18	0.56	0.50	0.33
SP	2008	27	64.5957	165.6092	308.5	31.1	34	0.44	0.35	0.12
SP	2008	28	64.6384	164.1304	377.6	39.9	28	0.50	0.43	0.21
SP	2008	29	64.8336	163.7948	336.8	46.1	18	0.61	0.56	0.22
SP	2008	30	64.6782	165.8808	277.7	5.9	18	0.56	0.56	0.17

[a]All coordinates recorded in WGS1984.

[b]Sex and age were classified by horn size and development; individuals >4 y were considered adults.

Table D.2. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) in 2 populations in northern Alaska, late winter, 2007-2008 (pgs. 186-188).

Population	North Slope						Cape Thompson		
Year	2007			2008			2007		
Site no. (10 fecal samples per site)	32	33	34	35	36	37	38	39	40
Mosses	54.0	24.9	34.8	29.5	7.3	24.4	25.3	10.0	43.4
Cetraria and *Dactylina* spp.	1.5	0.9	0.0	0.9	0.5	4.2	0.9	0.0	3.4
Cladina and *Cladonia* spp.	1.5	0.9	0.1	0.9	0.0	4.0	0.9	0.5	1.2
Nephroma spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Peltigera and *Lobaria* spp.	1.5	0.9	0.0	0.0	0.0	0.0	0.9	0.5	1.2
Stereocaulon spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.5	0.0
Carex spp.	14.0	28.1	20.8	12.3	7.9	21.8	38.5	50.4	16.3
Eriophorum spp.	9.5	27.8	19.7	8.6	10.1	33.6	10.5	3.8	2.3
Juncus spp.	1.9	7.7	4.2	0.0	0.0	1.5	6.7	4.4	2.3
Luzula spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alopecurus spp.	0.0	0.0	0.0	0.0	5.9	0.8	0.0	0.0	0.0
Arctagrostis spp.	0.6	0.0	0.0	0.0	2.5	0.8	0.0	0.0	1.9
Arctophila spp.	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bromus spp.	0.6	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Calamagrostis spp.	0.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Deschampsia spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Elymus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Festuca spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hierochloe spp.	0.6	0.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0
Poa spp.	0.6	0.0	0.0	0.0	4.2	0.0	0.9	1.0	4.8
Puccinellia spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Unknown grass	0.5	0.7	0.8	1.1	4.8	1.1	0.3	1.6	1.4

Table D.2. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) in 2 populations in northern Alaska, late winter, 2007-2008 (pgs. 186-188).

Population	North Slope						Cape Thompson		
Year	2007			2008			2007		
Site no. (10 fecal samples per site)	32	33	34	35	36	37	38	39	40
Allium spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Antennaria spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cerastium spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Equisetum spp.	1.5	0.2	16.0	23.1	4.8	0.0	0.0	0.6	0.0
Lupinus spp.	1.5	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0
Lycopodium spp.	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Oxytropis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Phlox spp.	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Potentilla spp.	0.0	0.0	0.0	0.5	1.6	0.5	0.0	3.0	0.0
Pyrola spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Saxifraga spp.	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Silene spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Stellaria spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Unknown forb	0.8	0.0	0.0	0.9	0.0	0.6	0.0	1.7	1.0
Arctostaphylos spp.	0.4	0.0	0.0	0.0	0.6	1.2	0.8	0.7	0.8
Betula spp.	0.4	0.5	1.0	2.6	16.6	0.0	0.8	5.8	0.8
Cassiope spp.	0.4	0.0	0.0	1.3	0.0	0.0	0.0	0.7	0.8
Dryas spp.	0.8	1.0	1.0	4.4	5.3	1.2	8.4	1.4	3.5
Empetrum spp.	0.4	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.8
Ledumleaf spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Loiseleuria spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhododendron spp.	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.8

Table D.2. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) in 2 populations in northern Alaska, late winter, 2007-2008 (pgs. 186-188).

Population	North Slope						Cape Thompson		
Year	2007			2008			2007		
Site no. (10 fecal samples per site)	32	33	34	35	36	37	38	39	40
Salix spp.	3.3	4.1	1.0	10.5	19.7	3.6	0.8	8.7	7.1
Vaccinium spp.	0.8	1.0	0.0	1.3	3.1	0.0	0.8	0.0	4.3
Unknown shrub	0.2	0.7	0.2	0.4	0.5	0.4	1.9	1.1	1.1
Ferns	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0

Table D.3. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) on the Seward Peninsula, Alaska, late winter, 2005-2006 (pgs. 189-190).

Year	2005					2006							
Site no.	8	9	10	11	12	13	14	15	16	17	18	19	20
Fecal samples per site	4	4	4	4	4	10	15	11	10	10	10	10	10
Mosses	25.4	48.8	52.2	51.5	67.0	57.9	36.1	14.4	60.0	37.0	50.5	40.7	37.6
Cetraria and *Dactylina* spp.	10.6	3.7	0.8	0.8	1.6	0.0	7.6	1.7	6.7	3.2	1.1	4.5	6.9
Cladina and *Cladonia* spp.	21.5	8.3	12.9	4.0	1.6	3.9	25.7	24.9	4.9	16.3	21.7	9.3	13.7
Nephroma spp.	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.2
Peltigera and *Lobaria* spp.	16.3	5.1	6.8	6.2	1.6	0.3	5.5	4.6	5.1	3.0	4.3	12.7	5.5
Stereocaulon spp.	1.1	0.3	0.0	0.8	0.0	0.3	1.3	1.7	0.5	0.6	1.1	0.6	1.2
Carex spp.	3.2	14.2	10.3	12.6	8.5	22.4	14.3	27.3	11.9	23.2	6.2	9.4	11.9
Eriophorum spp.	1.0	2.6	1.6	1.6	1.1	6.5	3.2	9.7	5.2	8.0	1.1	1.2	6.1
Juncus spp.	1.0	0.0	1.6	1.6	1.1	3.5	1.7	4.2	2.3	2.0	1.1	1.2	4.3
Luzula spp.	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.2
Alopecurus spp.	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arctagrostis spp.	0.6	1.0	0.7	0.7	1.1	0.0	0.0	0.0	0.0	0.0	0.8	0.7	0.7
Bromus spp.	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calamagrostis spp.	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Deschampsia spp.	0.6	1.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.8	0.7	0.0
Elymus spp.	0.0	0.0	0.7	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Hierochloe spp.	0.0	0.0	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Poa spp.	0.6	1.0	4.1	8.5	3.2	0.2	0.0	0.5	0.0	0.2	0.8	0.7	0.7
Puccinellia spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Unknown grass	0.8	0.3	0.6	0.5	2.2	0.5	0.2	0.4	0.3	0.8	0.4	0.8	0.5
Allium spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Antennaria spp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table D.3. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) on the Seward Peninsula, Alaska, late winter, 2005-2006 (pgs. 189-190).

Year	2005					2006							
Site no.	8	9	10	11	12	13	14	15	16	17	18	19	20
Fecal samples per site	4	4	4	4	4	10	15	11	10	10	10	10	10
Cerastium spp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Equisetum spp.	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.4	0.2	0.7	0.4	0.0
Lupinus spp.	0.5	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.7	0.4	0.1
Pyrola spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Saxifraga spp.	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.3	0.0	0.0	0.0	0.4	0.0
Silene spp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stellaria spp.	0.5	0.1	0.2	0.4	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Unknown forb	1.5	0.6	0.3	0.2	1.0	0.6	0.3	0.7	0.4	0.4	0.5	1.3	0.2
Arctostaphylos spp.	1.0	1.1	0.0	0.0	0.5	0.0	0.0	0.5	0.0	0.0	0.5	0.9	0.0
Betula spp.	1.0	0.0	0.0	0.0	0.5	0.0	0.4	3.7	0.4	0.0	0.0	1.8	1.2
Cassiope spp.	0.0	1.1	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.7	0.5	0.0	0.0
Dryas spp.	6.0	3.3	1.3	2.7	1.0	0.5	0.4	1.1	0.8	1.3	3.7	1.8	3.3
Empetrum spp.	1.0	1.1	1.3	1.4	0.5	0.0	0.0	0.5	0.4	1.3	0.5	0.0	1.2
Loiseleuria spp.	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Salix spp.	3.3	2.3	1.3	3.9	1.0	1.0	0.4	1.1	0.4	0.7	1.0	4.3	0.0
Vaccinium spp.	1.0	2.3	1.3	1.4	0.5	0.5	0.8	1.1	0.0	0.7	0.5	1.8	2.4
Unknown shrub	0.3	0.7	0.1	0.6	0.2	0.0	0.0	0.9	0.3	0.5	0.8	1.6	0.3

Table D.4. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) on the Seward Peninsula, Alaska, late winter, 2007-2008 (pgs. 191-192).

Year	2007					2008					
Site no.	21	22	23	24	25	26	27	28	29	30	31
Fecal samples per site	10	10	10	10	10	10	10	10	10	10	10
Mosses	39.9	52.5	52.9	30.2	33.0	28.4	18.8	34.3	42.6	41.4	42.0
Cetraria and *Dactylina* spp.	5.1	1.4	3.4	11.2	8.5	6.9	9.5	11.0	10.9	12.8	6.3
Cladina and *Cladonia* spp.	19.9	1.4	12.1	29.8	18.9	18.5	26.1	28.0	11.9	27.2	24.4
Nephroma spp.	0.1	0.0	0.2	0.4	0.4	0.0	0.0	0.0	0.2	1.6	0.0
Peltigera and *Lobaria* spp.	7.8	1.4	3.4	8.0	10.7	0.0	0.0	0.0	0.2	1.6	0.0
Stereocaulon spp.	0.1	1.4	0.0	0.4	0.4	4.7	2.7	3.2	4.3	3.5	3.1
Carex spp.	7.4	14.1	13.9	1.2	7.2	7.1	3.9	3.0	0.8	0.7	8.1
Eriophorum spp.	0.0	1.5	2.2	1.2	0.5	0.7	0.5	0.4	0.8	0.0	1.1
Juncus spp.	0.0	1.5	2.2	1.2	0.5	0.7	0.0	0.0	0.0	0.7	1.1
Luzula spp.	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arctagrostis spp.	0.0	0.0	0.5	0.9	0.0	0.5	0.0	0.0	0.4	0.0	1.2
Arctophila spp.	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.0	0.0
Elymus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Festuca spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0
Hierochloe spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Poa spp.	0.7	0.8	0.5	0.9	3.0	0.0	2.0	4.8	0.4	0.4	1.2
Puccinellia spp.	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown grass	0.6	0.9	0.4	0.6	1.0	0.0	0.5	0.0	0.2	0.8	1.4
Equisetum spp.	0.8	14.2	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lupinus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Lycopodium spp.	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Potentilla spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0

Table D.4. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups of muskoxen (sites) on the Seward Peninsula, Alaska, late winter, 2007-2008 (pgs. 191-192).

Year	2007					2008					
Site no.	21	22	23	24	25	26	27	28	29	30	31
Fecal samples per site	10	10	10	10	10	10	10	10	10	10	10
Pyrola spp.	0.0	0.5	0.0	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Saxifraga spp.	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stellaria spp.	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown forb	0.8	0.7	0.0	0.3	0.3	0.0	0.5	0.2	1.2	0.6	0.4
Arctostaphylos spp.	0.9	0.8	0.0	1.4	1.5	1.8	1.7	1.1	3.1	1.0	1.1
Betula spp.	0.0	0.0	0.9	1.4	1.5	1.8	3.4	0.0	1.4	1.0	0.0
Cassiope spp.	0.9	0.0	0.9	1.4	1.5	1.8	6.1	1.1	0.0	0.0	0.0
Dryas spp.	4.2	1.7	1.7	2.8	3.0	16.5	8.3	6.6	5.7	2.0	1.1
Empetrum spp.	0.9	0.8	0.9	1.4	1.5	0.0	1.7	0.0	0.0	1.0	0.0
Ledum spp.	0.0	0.0	0.0	0.0	0.0	1.8	1.7	1.1	1.4	1.0	1.1
Salix spp.	5.4	1.7	0.9	2.8	3.0	4.9	5.8	2.2	12.6	2.0	2.2
Vaccinium spp.	1.8	0.8	1.7	0.0	3.0	3.5	3.4	1.1	1.4	0.0	1.1
Unknown shrub	1.4	0.2	0.6	2.1	0.5	0.7	0.2	0.0	0.0	0.4	0.8

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
NS	2007	32	0.72	3.02	0.88	1.12	1.42
NS	2007	32	-1.93	5.10	0.20	0.42	0.57
NS	2007	32	1.09	5.55	0.64	0.79	0.92
NS	2007	32	-3.89	5.74	-0.08	0.13	0.31
NS	2007	32	1.12	5.06	0.70	0.85	1.00
NS	2007	32	-2.30	5.90	0.14	0.33	0.50
NS	2007	32	0.42	5.73	0.50	0.69	0.80
NS	2007	32	-3.34	4.86	0.00	0.23	0.40
NS	2007	32	0.38	5.51	0.54	0.70	0.84
NS	2007	32	-3.23	4.72	0.03	0.25	0.43
NS	2007	33	-3.28	5.85	-0.27	0.13	0.39
NS	2007	33	-2.73	5.89	-0.09	0.21	0.41
NS	2007	33	-3.35	6.22	-0.22	0.11	0.34
NS	2007	33	-3.48	5.77	-0.28	0.10	0.35
NS	2007	33	-4.88	5.73	-0.57	-0.10	0.18
NS	2007	33	-2.84	6.60	-0.08	0.17	0.37
NS	2007	33	-3.21	6.03	-0.29	0.13	0.38
NS	2007	33	-3.60	6.39	-0.35	0.08	0.30
NS	2007	33	-3.92	5.56	-0.52	0.03	0.36
NS	2007	34	-3.83	4.32	-0.16	0.08	0.28
NS	2007	34	-2.46	4.83	0.06	0.29	0.46
NS	2007	34	-5.14	4.42	-0.52	-0.15	0.08
NS	2007	34	-2.13	4.48	0.16	0.37	0.56
NS	2007	34	-3.79	4.67	-0.16	0.09	0.28
NS	2007	34	-2.46	4.74	0.07	0.30	0.49
NS	2007	34	-2.20	5.00	0.13	0.33	0.49
NS	2007	34	-4.44	2.39	-0.52	-0.04	0.29
NS	2007	34	-3.77	4.84	-0.20	0.09	0.28
NS	2008	34	-2.69	5.16	0.26	0.37	0.48
NS	2008	35	-2.92	4.45	0.21	0.37	0.50
NS	2008	35	-1.76	3.32	0.46	0.63	0.85
NS	2008	35	-2.38	3.17	0.37	0.54	0.72
NS	2008	35	-2.26	2.20	0.46	0.68	0.95
NS	2008	35	-3.50	3.60	0.18	0.33	0.48
NS	2008	35	-3.09	3.91	0.23	0.38	0.52
NS	2008	35	-1.99	2.44	0.51	0.70	0.95
NS	2008	35	-2.53	3.17	0.34	0.52	0.70

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
NS	2008	35	-1.16	1.46	0.80	1.07	1.56
NS	2008	35	-3.44	3.08	0.21	0.41	0.58
NS	2008	36	-2.19	2.81	0.49	0.64	0.86
NS	2008	36	-1.95	2.91	0.50	0.67	0.87
NS	2008	36	-2.49	2.06	0.46	0.67	0.97
NS	2008	36	-3.70	1.43	0.24	0.49	0.80
NS	2008	36	-2.30	3.23	0.06	0.35	0.63
NS	2008	36	-4.73	3.75	-0.61	-0.21	0.04
NS	2008	36	-2.87	2.71	-0.07	0.26	0.54
NS	2008	36	-4.24	2.67	-0.57	-0.13	0.18
NS	2008	36	-2.53	2.17	-0.08	0.41	0.80
NS	2008	36	-1.71	3.85	0.21	0.44	0.67
NS	2008	37	-2.01	4.21	0.10	0.35	0.54
NS	2008	37	-2.23	3.90	0.09	0.32	0.54
NS	2008	37	-2.02	3.28	0.15	0.42	0.68
NS	2008	37	-4.00	3.28	-0.42	-0.06	0.21
CT	2007	37	-0.02	5.64	0.36	0.64	0.84
CT	2007	37	-4.88	4.42	-0.43	0.01	0.38
CT	2007	37	-4.52	4.95	-0.31	0.06	0.40
CT	2007	37	3.30	4.17	0.88	1.34	2.48
CT	2007	37	-5.90	3.64	-1.13	-0.17	0.27
CT	2007	37	-6.12	4.10	-0.86	-0.19	0.16
CT	2007	38	-4.36	4.05	-0.34	0.10	0.46
CT	2007	38	-4.17	5.66	-0.22	0.10	0.36
CT	2007	38	-1.98	5.86	0.12	0.38	0.60
CT	2007	38	-2.88	5.23	0.05	0.30	0.51
CT	2007	38	-3.77	4.72	-0.12	0.19	0.47
CT	2007	38	-1.43	4.93	0.22	0.51	0.79
CT	2007	38	-3.53	3.87	-0.06	0.26	0.68
CT	2007	38	-2.84	4.49	0.03	0.34	0.64
CT	2007	38	-0.88	4.66	0.31	0.62	0.96
CT	2007	38	-3.97	5.14	-0.07	0.15	0.41
CT	2007	39	-3.87	3.92	-0.09	0.20	0.58
CT	2007	39	-5.50	4.69	-0.31	-0.05	0.18
CT	2007	39	-4.50	5.02	-0.14	0.09	0.31
CT	2007	39	-2.84	5.58	0.05	0.29	0.48
CT	2007	39	-3.65	4.70	-0.03	0.21	0.50

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
CT	2007	39	-5.46	5.09	-0.27	-0.05	0.19
CT	2007	39	-3.22	5.27	0.03	0.25	0.45
CT	2007	39	-3.50	5.58	0.01	0.21	0.41
CT	2007	39	-4.21	5.04	-0.11	0.13	0.36
CT	2007	39	-3.87	4.95	-0.07	0.17	0.42
CT	2007	40	-4.96	5.68	-0.24	0.02	0.24
SP	2005	1	0.07	6.85	0.50	0.61	0.71
SP	2005	1	0.15	5.37	0.59	0.73	0.85
SP	2005	1	-0.27	8.54	0.34	0.46	0.56
SP	2005	2	-2.51	5.81	0.16	0.30	0.42
SP	2005	2	-0.70	6.13	0.37	0.51	0.65
SP	2005	3	2.28	5.84	0.82	0.93	1.05
SP	2005	3	-2.91	6.43	0.20	0.33	0.46
SP	2005	3	1.40	5.83	0.72	0.83	0.94
SP	2005	3	-3.08	6.26	0.21	0.32	0.43
SP	2005	5	-1.59	6.94	0.34	0.45	0.57
SP	2005	5	-1.45	6.75	0.37	0.47	0.58
SP	2005	5	-1.12	6.51	0.40	0.52	0.62
SP	2005	5	1.82	6.73	0.69	0.80	0.92
SP	2005	6	1.80	6.24	0.74	0.84	0.94
SP	2005	6	-1.99	7.10	0.28	0.40	0.51
SP	2005	6	2.50	6.72	0.74	0.87	0.98
SP	2005	6	-2.28	6.32	0.31	0.41	0.51
SP	2005	7	-1.67	6.27	0.37	0.47	0.59
SP	2005	7	-2.50	6.13	0.27	0.39	0.51
SP	2005	7	-5.02	6.36	-0.02	0.11	0.22
SP	2005	7	-1.93	6.06	0.34	0.45	0.56
SP	2005	9	-4.04	4.68	0.16	0.30	0.45
SP	2005	9	-0.94	5.46	0.50	0.62	0.73
SP	2005	9	-4.24	5.37	0.13	0.25	0.37
SP	2005	10	-3.04	4.90	0.22	0.39	0.53
SP	2005	11	2.30	6.21	0.80	0.91	0.99
SP	2005	11	-2.34	4.27	0.46	0.57	0.69
SP	2005	11	1.55	4.43	0.88	1.00	1.15
SP	2005	12	-2.27	4.18	0.29	0.45	0.60
SP	2005	12	-2.39	4.28	0.26	0.43	0.59
SP	2006	13	-1.62	5.29	0.18	0.38	0.55

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
SP	2006	13	-2.32	4.77	0.07	0.30	0.48
SP	2006	13	0.32	5.53	0.50	0.66	0.81
SP	2006	13	0.14	6.08	0.42	0.58	0.73
SP	2006	13	1.23	5.88	0.60	0.76	0.90
SP	2006	13	-1.88	5.48	0.17	0.33	0.48
SP	2006	13	-1.16	5.48	0.27	0.44	0.61
SP	2006	13	-3.03	6.03	-0.06	0.14	0.30
SP	2006	13	-2.29	6.55	0.05	0.23	0.38
SP	2006	14	0.35	5.34	0.61	0.74	0.87
SP	2006	14	-0.10	4.31	0.65	0.79	0.95
SP	2006	14	-3.47	4.85	0.13	0.28	0.42
SP	2006	14	-2.19	5.33	0.28	0.43	0.55
SP	2006	14	-2.33	5.20	0.27	0.42	0.54
SP	2006	14	-0.22	5.05	0.56	0.70	0.82
SP	2006	14	-0.36	4.39	0.58	0.74	0.89
SP	2006	14	0.31	4.84	0.66	0.79	0.92
SP	2006	14	2.27	4.59	0.94	1.08	1.25
SP	2006	14	0.93	4.23	0.80	0.95	1.14
SP	2006	14	-0.53	4.38	0.58	0.72	0.86
SP	2006	14	0.64	5.08	0.68	0.81	0.94
SP	2006	14	-0.16	4.66	0.60	0.74	0.88
SP	2006	14	-0.78	4.75	0.49	0.65	0.78
SP	2006	14	-1.52	4.98	0.38	0.53	0.65
SP	2006	15	-1.13	5.85	0.31	0.44	0.61
SP	2006	15	-3.03	5.26	0.05	0.20	0.36
SP	2006	15	-1.61	5.64	0.25	0.39	0.53
SP	2006	15	-2.93	5.71	0.05	0.21	0.34
SP	2006	15	-4.00	5.72	-0.13	0.06	0.21
SP	2006	15	-2.68	5.78	0.09	0.24	0.39
SP	2006	15	-3.34	5.70	-0.03	0.15	0.29
SP	2006	15	-3.24	5.52	0.00	0.17	0.32
SP	2006	15	-3.57	5.34	-0.04	0.12	0.28
SP	2006	16	1.46	6.47	0.59	0.73	0.86
SP	2006	16	1.80	6.10	0.68	0.81	0.94
SP	2006	16	1.74	6.38	0.65	0.78	0.91
SP	2006	17	2.15	5.86	0.75	0.89	1.04
SP	2006	17	3.48	5.88	0.92	1.07	1.23

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
SP	2006	18	-1.61	3.60	0.59	0.72	0.84
SP	2006	18	-2.93	4.31	0.40	0.51	0.63
SP	2006	18	-4.00	3.96	0.29	0.41	0.52
SP	2006	18	-2.68	3.24	0.49	0.62	0.78
SP	2006	18	-3.34	3.83	0.37	0.50	0.60
SP	2006	18	-3.24	3.96	0.37	0.50	0.64
SP	2006	18	-6.08	3.93	0.02	0.17	0.29
SP	2006	18	-3.57	4.31	0.33	0.44	0.57
SP	2006	19	-1.30	5.24	0.50	0.61	0.73
SP	2006	19	-4.80	3.73	0.13	0.27	0.41
SP	2006	19	-2.08	4.30	0.47	0.58	0.70
SP	2006	19	-3.42	4.45	0.29	0.41	0.55
SP	2006	19	-3.48	4.43	0.27	0.41	0.52
SP	2006	19	-4.05	3.97	0.22	0.36	0.50
SP	2006	19	-3.06	3.98	0.36	0.48	0.62
SP	2006	19	-5.04	4.22	0.10	0.23	0.34
SP	2006	19	-3.80	4.32	0.24	0.38	0.51
SP	2006	19	-2.87	4.74	0.34	0.46	0.59
SP	2006	19	-4.82	4.88	0.11	0.24	0.34
SP	2006	19	-5.00	4.21	0.07	0.23	0.36
SP	2006	20	-2.33	4.81	0.34	0.47	0.60
SP	2006	20	-3.48	4.67	0.20	0.34	0.46
SP	2006	20	-1.25	4.66	0.49	0.62	0.75
SP	2006	20	-0.46	4.07	0.64	0.78	0.93
SP	2006	20	-2.29	4.49	0.38	0.50	0.64
SP	2006	20	-3.02	4.95	0.24	0.38	0.50
SP	2006	20	-1.99	4.90	0.35	0.51	0.62
SP	2007	21	-6.83	4.70	-0.04	0.07	0.19
SP	2007	21	-2.36	4.32	0.47	0.58	0.69
SP	2007	21	-4.74	4.27	0.18	0.31	0.42
SP	2007	21	-5.30	3.90	0.14	0.26	0.38
SP	2007	21	-5.60	4.12	0.08	0.22	0.33
SP	2007	21	-7.34	4.50	-0.11	0.02	0.13
SP	2007	21	-8.08	4.90	-0.18	-0.06	0.05
SP	2007	21	-3.71	4.34	0.31	0.42	0.54
SP	2007	22	-5.14	4.61	-0.07	0.08	0.23
SP	2007	22	-3.56	4.62	0.16	0.29	0.43

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
SP	2007	22	-2.75	5.08	0.25	0.38	0.53
SP	2007	22	-4.14	5.95	0.05	0.18	0.29
SP	2007	22	-3.95	5.01	0.09	0.23	0.36
SP	2007	22	-4.19	5.16	0.05	0.19	0.33
SP	2007	22	-3.80	4.86	0.12	0.25	0.38
SP	2007	22	-3.33	4.96	0.17	0.30	0.45
SP	2007	22	-2.54	4.28	0.29	0.45	0.61
SP	2007	22	-2.97	4.63	0.22	0.37	0.51
SP	2007	23	-1.83	4.21	0.42	0.58	0.73
SP	2007	23	-0.90	4.99	0.51	0.64	0.76
SP	2007	23	-3.59	4.76	0.14	0.32	0.48
SP	2007	23	-3.28	4.70	0.15	0.36	0.50
SP	2007	23	-1.19	5.39	0.42	0.57	0.69
SP	2007	23	-2.94	4.67	0.24	0.40	0.53
SP	2007	23	-3.33	4.57	0.15	0.36	0.50
SP	2007	23	-3.96	5.40	0.09	0.25	0.41
SP	2007	23	-3.81	5.31	0.08	0.27	0.41
SP	2007	23	-2.71	5.10	0.25	0.41	0.54
SP	2007	24	-2.99	3.70	0.40	0.53	0.65
SP	2007	24	-4.14	4.47	0.21	0.35	0.47
SP	2007	24	-3.53	4.17	0.33	0.43	0.56
SP	2007	24	-4.63	3.48	0.19	0.33	0.47
SP	2007	24	-3.61	4.11	0.29	0.43	0.55
SP	2007	24	-4.13	4.48	0.23	0.35	0.48
SP	2007	24	-4.64	4.19	0.17	0.30	0.43
SP	2007	24	-4.25	4.37	0.20	0.34	0.46
SP	2007	24	-2.60	4.31	0.40	0.54	0.65
SP	2007	24	-3.18	3.65	0.37	0.51	0.63
SP	2007	25	-2.87	3.92	0.28	0.52	0.66
SP	2007	25	-1.92	4.07	0.48	0.62	0.78
SP	2007	25	-0.53	4.60	0.63	0.75	0.87
SP	2007	25	-1.94	4.31	0.44	0.60	0.72
SP	2007	25	-2.13	4.47	0.43	0.57	0.70
SP	2007	25	-0.71	4.67	0.60	0.72	0.85
SP	2007	25	-0.88	3.98	0.62	0.76	0.88
SP	2007	25	-0.82	4.14	0.62	0.75	0.90
SP	2007	25	-0.68	4.44	0.61	0.74	0.87

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
SP	2008	26	-1.86	4.98	0.41	0.53	0.67
SP	2008	26	-1.33	3.72	0.53	0.70	0.87
SP	2008	26	-0.86	2.64	0.72	0.90	1.11
SP	2008	26	-1.63	3.02	0.55	0.73	0.93
SP	2008	26	-2.22	3.65	0.40	0.58	0.75
SP	2008	26	-1.52	4.20	0.48	0.63	0.78
SP	2008	26	-0.51	2.73	0.74	0.95	1.18
SP	2008	26	0.67	4.76	0.64	0.83	0.97
SP	2008	26	0.35	5.83	0.51	0.67	0.81
SP	2008	26	0.14	5.14	0.54	0.70	0.87
SP	2008	27	0.19	4.19	0.70	0.85	1.00
SP	2008	27	0.29	4.31	0.70	0.85	0.99
SP	2008	27	0.21	4.43	0.67	0.82	0.96
SP	2008	27	0.13	3.77	0.73	0.89	1.05
SP	2008	27	0.34	5.09	0.65	0.77	0.90
SP	2008	27	0.06	4.56	0.66	0.79	0.95
SP	2008	27	0.27	4.56	0.64	0.82	0.95
SP	2008	27	0.22	5.56	0.58	0.72	0.84
SP	2008	27	0.16	4.49	0.67	0.81	0.95
SP	2008	27	0.42	4.41	0.71	0.85	1.00
SP	2008	28	-1.27	4.55	0.45	0.60	0.76
SP	2008	28	-0.12	3.60	0.67	0.88	1.06
SP	2008	28	-1.08	3.19	0.59	0.78	0.98
SP	2008	28	-1.06	4.52	0.47	0.64	0.79
SP	2008	28	-2.33	3.38	0.33	0.55	0.74
SP	2008	28	-1.50	4.74	0.40	0.56	0.70
SP	2008	28	-2.58	4.45	0.26	0.43	0.61
SP	2008	28	-1.87	4.51	0.37	0.53	0.68
SP	2008	28	0.57	3.52	0.83	0.99	1.24
SP	2008	28	-1.68	4.62	0.33	0.49	0.67
SP	2008	29	-0.79	4.84	0.47	0.61	0.76
SP	2008	29	-0.43	5.07	0.50	0.64	0.78
SP	2008	29	-1.90	4.66	0.30	0.46	0.60
SP	2008	29	-2.35	4.48	0.24	0.40	0.56
SP	2008	29	-0.93	5.02	0.46	0.57	0.71
SP	2008	29	-1.40	4.52	0.37	0.55	0.71
SP	2008	29	-1.67	5.02	0.27	0.47	0.61

Table D.5. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 261$) and the simulated values of the proportion of urea N derived from body N (p-UN) for muskoxen in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, late winter, 2005-2008 (pgs. 193-200).

Population	Year	Site no.	$\delta^{15}N$		p-UN		
			Urea	Body	Minimum	Median	Maximum
SP	2008	29	-1.32	5.05	0.37	0.52	0.67
SP	2008	29	-0.19	5.59	0.47	0.62	0.76

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
NS	2007	32	1.97
NS	2007	32	1.13
NS	2007	32	0.47
NS	2007	32	1.12
NS	2007	32	0.06
NS	2007	32	0.53
NS	2007	32	1.14
NS	2007	32	0.26
NS	2007	32	0.09
NS	2007	32	1.39
NS	2007	33	1.77
NS	2007	33	1.77
NS	2007	33	1.34
NS	2007	33	0.52
NS	2007	33	-0.03
NS	2007	33	0.51
NS	2007	33	1.40
NS	2007	33	2.48
NS	2007	33	3.02
NS	2007	33	2.59
NS	2007	34	0.63
NS	2007	34	0.79
NS	2007	34	1.26
NS	2007	34	2.06
NS	2007	34	1.48
NS	2007	34	1.69
NS	2007	34	1.51
NS	2007	34	1.41
NS	2007	34	1.95
NS	2007	34	1.33
NS	2008	34	0.37
NS	2008	35	0.23
NS	2008	35	0.06
NS	2008	35	0.18
NS	2008	23	0.20
NS	2008	35	0.10
NS	2008	35	0.22
NS	2008	35	0.53

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
NS	2008	35	-0.14
NS	2008	35	0.05
NS	2008	23	-0.46
NS	2008	23	-0.31
NS	2008	35	-0.66
NS	2008	35	-0.28
NS	2008	36	-0.10
NS	2008	23	0.45
NS	2008	24	-0.21
NS	2008	36	-0.18
NS	2008	36	-0.15
NS	2008	36	0.33
NS	2008	36	2.45
NS	2008	36	1.78
NS	2008	36	2.21
NS	2008	36	1.69
NS	2008	36	1.53
NS	2008	36	2.18
NS	2008	37	1.79
NS	2008	37	1.51
NS	2008	37	2.44
NS	2008	37	2.22
CT	2007	24	-1.10
CT	2007	37	-0.16
CT	2007	37	0.49
CT	2007	37	0.50
CT	2007	37	0.57
CT	2007	37	1.01
CT	2007	37	1.11
CT	2007	38	1.37
CT	2007	38	1.37
CT	2007	38	1.45
CT	2007	38	0.12
CT	2007	38	0.21
CT	2007	38	0.35
CT	2007	38	0.37
CT	2007	38	0.43
CT	2007	38	0.48

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
CT	2007	28	0.54
CT	2007	29	0.80
CT	2007	38	1.14
CT	2007	39	1.40
CT	2007	39	0.27
CT	2007	39	0.38
CT	2007	39	0.45
CT	2007	39	0.54
CT	2007	39	0.55
CT	2007	39	0.55
CT	2007	39	0.55
CT	2007	39	0.65
CT	2007	39	0.81
CT	2007	40	0.86
SP	2005	2	1.00
SP	2005	8	-1.43
SP	2005	8	-1.04
SP	2005	8	-0.79
SP	2005	8	-0.61
SP	2005	9	-1.08
SP	2005	9	-0.89
SP	2005	9	-0.82
SP	2005	9	-0.48
SP	2005	10	-1.23
SP	2005	10	-0.44
SP	2005	10	-0.22
SP	2005	10	-0.15
SP	2005	11	-1.83
SP	2005	11	-1.73
SP	2005	11	-1.58
SP	2005	11	-1.46
SP	2005	12	0.33
SP	2005	12	0.97
SP	2005	12	0.33
SP	2006	13	0.94
SP	2006	13	1.22
SP	2006	13	1.37
SP	2006	13	1.62

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
SP	2006	13	1.67
SP	2006	13	1.84
SP	2006	13	1.85
SP	2006	13	1.94
SP	2006	13	2.03
SP	2006	13	2.16
SP	2006	14	-0.60
SP	2006	14	-0.33
SP	2006	14	-0.22
SP	2006	14	0.01
SP	2006	14	0.06
SP	2006	14	0.06
SP	2006	14	0.11
SP	2006	14	0.13
SP	2006	14	0.19
SP	2006	14	0.31
SP	2006	14	0.35
SP	2006	14	0.36
SP	2006	14	0.40
SP	2006	14	0.52
SP	2006	15	0.73
SP	2006	15	1.00
SP	2006	15	1.25
SP	2006	15	1.31
SP	2006	15	1.34
SP	2006	15	1.35
SP	2006	15	1.44
SP	2006	15	1.44
SP	2006	15	1.47
SP	2006	15	1.55
SP	2006	15	1.70
SP	2006	16	0.88
SP	2006	16	1.32
SP	2006	16	1.40
SP	2006	16	1.42
SP	2006	16	1.46
SP	2006	16	1.60
SP	2006	16	1.69

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
SP	2006	16	1.69
SP	2006	16	2.08
SP	2006	16	2.12
SP	2006	17	1.33
SP	2006	17	1.35
SP	2006	17	1.37
SP	2006	17	1.42
SP	2006	17	1.57
SP	2006	17	1.68
SP	2006	17	1.70
SP	2006	17	1.75
SP	2006	17	1.76
SP	2006	17	2.39
SP	2006	18	-2.05
SP	2006	18	-1.97
SP	2006	18	-1.95
SP	2006	18	-1.94
SP	2006	18	-1.91
SP	2006	18	-1.80
SP	2006	18	-1.80
SP	2006	18	-1.72
SP	2006	18	-1.59
SP	2006	18	-1.40
SP	2006	19	-1.51
SP	2006	19	-1.48
SP	2006	19	-1.42
SP	2006	19	-1.20
SP	2006	19	-1.18
SP	2006	19	-1.14
SP	2006	19	-1.13
SP	2006	19	-0.98
SP	2006	19	-0.92
SP	2006	19	-0.69
SP	2006	20	-0.95
SP	2006	20	-0.64
SP	2006	20	-0.47
SP	2006	20	-0.36
SP	2006	20	-0.35

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
SP	2006	20	-0.33
SP	2006	20	-0.30
SP	2006	20	-0.25
SP	2006	20	-0.20
SP	2006	20	-0.18
SP	2006	20	-0.17
SP	2007	21	-1.56
SP	2007	21	-2.09
SP	2007	21	-1.87
SP	2007	21	-1.87
SP	2007	21	-1.79
SP	2007	21	-1.77
SP	2007	21	-1.75
SP	2007	21	-1.73
SP	2007	21	-1.72
SP	2007	21	-1.65
SP	2007	22	-0.27
SP	2007	22	-0.14
SP	2007	22	-0.13
SP	2007	22	-0.02
SP	2007	22	0.00
SP	2007	22	0.01
SP	2007	22	0.07
SP	2007	22	0.16
SP	2007	22	0.18
SP	2007	22	0.31
SP	2007	23	-0.88
SP	2007	23	-0.84
SP	2007	23	-0.69
SP	2007	23	-0.60
SP	2007	23	-0.57
SP	2007	23	-0.48
SP	2007	23	-0.44
SP	2007	23	-0.09
SP	2007	23	0.12
SP	2007	23	0.61
SP	2007	24	-1.83
SP	2007	24	-1.80

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
SP	2007	24	-1.67
SP	2007	24	-1.58
SP	2007	24	-1.52
SP	2007	24	-1.49
SP	2007	24	-1.41
SP	2007	24	-1.41
SP	2007	24	-1.37
SP	2007	24	-0.78
SP	2007	25	-1.84
SP	2007	25	-1.78
SP	2007	25	-1.72
SP	2007	25	-1.62
SP	2007	25	-1.50
SP	2007	25	-1.47
SP	2007	25	-1.41
SP	2007	25	-1.11
SP	2007	25	-0.88
SP	2007	25	0.01
SP	2008	26	-0.41
SP	2008	26	0.12
SP	2008	26	-0.42
SP	2008	26	-1.10
SP	2008	26	-1.54
SP	2008	26	-1.35
SP	2008	26	-0.66
SP	2008	26	-0.88
SP	2008	26	0.20
SP	2008	26	-0.28
SP	2008	21	0.38
SP	2008	21	0.97
SP	2008	26	0.65
SP	2008	21	-0.14
SP	2008	21	1.52
SP	2008	26	0.75
SP	2008	26	0.95
SP	2008	22	0.95
SP	2008	22	1.15
SP	2008	26	1.64

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
SP	2008	27	-0.90
SP	2008	27	-0.61
SP	2008	27	0.66
SP	2008	27	0.13
SP	2008	27	-0.92
SP	2008	27	0.04
SP	2008	27	-0.03
SP	2008	27	-0.87
SP	2008	27	-0.07
SP	2008	27	-0.05
SP	2008	27	-0.12
SP	2008	28	-0.12
SP	2008	28	-0.11
SP	2008	28	-0.27
SP	2008	28	-0.47
SP	2008	28	-0.37
SP	2008	28	0.92
SP	2008	28	0.90
SP	2008	28	-0.44
SP	2008	28	-0.38
SP	2008	27	-0.33
SP	2008	27	0.17
SP	2008	22	-0.26
SP	2008	22	-0.39
SP	2008	22	0.63
SP	2008	22	-0.58
SP	2008	23	1.49
SP	2008	23	4.20
SP	2008	27	0.03
SP	2008	28	0.41
SP	2008	28	1.31
SP	2008	29	0.36
SP	2008	29	0.55
SP	2008	29	0.89
SP	2008	29	1.02
SP	2008	29	0.28
SP	2008	29	0.35
SP	2008	29	1.01

Table D.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 306) of muskox in the North Slope (NS), Cape Thompson (CT), and Seward Peninsula (SP) populations in northern Alaska, 2005-2008 (pgs. 201-209).

Population	Year	Site no.	$\delta^{15}N_{Fiber}$
SP	2008	29	0.72
SP	2008	29	0.81

Appendix E. Foraging sites, microhistology, and isotopes of N in the excreta of wild caribou in late winter

Table E.1. The locations and physiographic features of the sites used by groups of caribou in 4 populations [Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH)] in Alaska and Yukon Territory, late winter, 2006-2008 (pgs. 211-212).

Population	Year	Site no.	Latitude (N)[a]	Longitude (W)[a]	Elevation (m)	Slope (°)
CAH	2006	1	67.8578	148.1351	885.3	17.7
CAH	2006	2	67.5382	147.4113	578.5	2.6
CAH	2006	3	68.7060	148.3535	727.0	37.0
CAH	2006	4	69.1295	146.8218	883.9	6.2
CAH	2007	5	67.8421	151.7249	1,222.9	27.3
CAH	2007	6	69.0730	146.6878	1,139.7	29.5
CAH	2007	7	68.4966	149.4702	831.5	11.6
CAH	2007	8	68.3819	149.3111	846.7	18.1
CAH	2007	9	68.0118	149.7237	741.9	24.7
CAH	2008	10	69.5968	146.3135	221.9	6.8
CAH	2008	11	69.2386	147.2705	415.7	0.7
CAH	2008	12	68.6465	148.7320	616.0	2.6
WAH	2006	13	67.0497	156.5245	122.2	0.3
WAH	2006	14	67.0284	156.4338	120.9	0.9
WAH	2006	15	67.0708	156.5506	110.7	1.0
WAH	2006	16	67.0698	156.4720	106.4	0.9
WAH	2006	17	66.9445	157.1115	93.9	8.0
WAH	2007	18	65.3443	159.4642	524.3	7.7
WAH	2007	19	65.3403	159.4455	414.2	14.9
WAH	2007	20	65.2303	159.3494	353.9	33.7
WAH	2007	21	65.4942	159.3172	499.0	30.8
WAH	2007	22	65.4188	158.5737	435.3	19.7
WAH	2007	23	65.3814	158.5558	108.8	16.7
WAH	2008	24	66.8009	156.7014	64.6	1.1

Table E.1. The locations and physiographic features of the sites used by groups of caribou in 4 populations [Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH)] in Alaska and Yukon Territory, late winter, 2006-2008 (pgs. 211-212).

Population	Year	Site no.	Latitude (N)[a]	Longitude (W)[a]	Elevation (m)	Slope (°)
WAH	2008	25	67.0505	156.4354	111.6	11.7
WAH	2008	26	66.8404	156.1506	108.2	5.0
CH	2006	27	61.6495	141.0142	1,152.8	3.4
CH	2006	28	61.7233	140.7690	1,097.0	8.0
CH	2006	29	61.4182	140.3857	1,430.0	6.8
CH	2006	30	61.7033	140.7145	1,107.0	0.6
CH	2006	31	61.4748	140.4522	1,702.0	20.9
CH	2006	32	61.6683	140.6760	1,013.0	1.7
CH	2008	33	61.7114	140.7320	1,096.0	1.0
CH	2008	34	61.6493	141.0796	1,171.7	10.7
CH	2008	35	61.6463	141.1682	1,168.6	13.1
DH	2007	36	63.7669	150.0878	598.9	4.2
DH	2007	37	63.8356	149.8919	556.6	1.9
DH	2008	38	63.3908	151.6370	467.3	3.5
DH	2008	39	63.6843	150.2258	887.9	28.6

[b]All coordinates recorded in WGS1984.

Table E.2. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups (site) of caribou in the Central Arctic Herd in northern Alaska, late winter, 2006-2008 (pgs. 213-214).

Year	2006				2007				2008		
Site no.	1	2	3	4	5	6	7	8	10	11	12
Fecal samples per site	21	18	20	6	10	18	20	20	20	20	20
Total moss	30.1	14.5	16.0	23.4	40.7	38.2	67.6	30.8	55.7	34.3	37.0
Alectoria and *Bryoria* spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cetraria and *Dactylina* spp.	5.1	9.3	11.3	6.4	5.3	8.9	0.5	9.2	1.1	7.1	1.2
Cladina and *Cladonia* spp.	37.6	42.7	45.8	49.2	32.7	28.6	6.8	40.1	3.3	32.8	25.0
Peltigera spp.	6.2	12.1	7.8	6.4	9.6	6.5	5.5	9.7	3.5	7.4	5.6
Nephroma spp.	0.0	0.0	0.0	0.0	1.0	0.7	0.0	1.3	0.0	1.4	1.2
Stereocaulon spp.	0.8	1.6	1.6	1.5	1.0	0.7	0.0	1.3	1.1	1.4	1.2
Carex spp.	7.1	5.9	5.7	0.2	3.5	1.1	6.9	1.1	3.8	5.3	1.5
Eriophorum spp.	0.6	1.6	0.9	0.2	0.0	0.0	8.1	0.0	2.0	0.0	1.5
Juncus and *Luzula* spp.	0.0	0.0	0.9	0.0	0.0	0.0	0.6	0.0	0.0	0.3	1.5
Arctagrostis spp.	0.5	1.3	0.0	1.2	0.0	0.3	0.9	0.0	0.0	0.0	0.0
Bromus spp.	0.0	0.0	0.0	0.0	0.0	0.3	0.9	0.0	0.0	0.0	0.0
Calamagrostis spp.	0.0	1.3	0.6	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Poa spp.	0.0	1.3	0.6	0.0	0.0	0.0	0.9	0.3	0.6	0.0	0.2
Unknown grass	0.6	0.0	0.6	0.4	1.1	1.1	0.6	0.8	1.1	0.3	0.0
Antennaria spp.	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arenaria spp.	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Astragalus spp.	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0
Equisetum spp.	3.6	0.0	0.4	0.0	0.0	0.0	0.0	0.0	15.3	1.5	18.7
Lupinus and *Oxytropis* spp.	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.6	1.5	0.2
Lycopodium spp.	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stellaria spp.	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown forb	0.2	0.0	0.0	0.0	0.2	0.6	0.0	0.3	1.1	0.0	0.0
Alnus spp.	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0

Table E.2. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups (site) of caribou in the Central Arctic Herd in northern Alaska, late winter, 2006-2008 (pgs. 213-214).

Year	2006				2007				2008		
Site no.	1	2	3	4	5	6	7	8	10	11	12
Fecal samples per site	21	18	20	6	10	18	20	20	20	20	20
Andromeda and *Cassiope* spp.	0.0	0.9	0.7	1.3	0.9	5.4	0.0	0.8	1.1	0.6	0.9
Arctostaphylos spp.	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Betula spp.	1.1	0.9	0.7	1.3	0.0	0.7	0.0	0.8	1.1	0.6	0.9
Dryas spp.	1.1	0.9	1.4	0.0	0.0	0.7	0.0	0.0	3.1	1.3	0.0
Empetrum spp.	0.6	0.9	0.7	2.6	0.0	0.7	0.0	0.8	1.1	0.0	0.9
Ledum spp.	0.6	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.9
Rhododendron spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Salix spp.	1.1	1.8	1.4	2.6	1.8	0.7	0.8	1.7	1.1	1.3	0.9
Vaccinium spp.	1.1	1.8	1.4	2.6	1.8	0.7	0.0	0.8	1.1	1.3	0.9
Unknown shrub	0.6	0.2	0.0	0.5	0.0	0.9	0.0	0.0	0.7	0.9	0.0
Fern	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0

Table E.3. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups (site) of caribou in the Western Arctic Herd in northwest Alaska, late winter, 2006-2008 (pgs. 215-216).

Year	2006					2007						2008		
Site no.	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Fecal samples per site	23	24	23	19	19	20	20	20	20	10	10	20	20	18
Total moss	21.2	28.8	26.0	34.1	15.7	26.5	17.1	16.3	19.9	10.8	5.3	27.1	37.2	24.9
Alectoria and *Bryoria* spp.	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cetraria and *Dactylina* spp.	6.1	5.5	7.3	5.0	8.1	3.5	8.4	5.9	8.1	3.6	5.6	1.5	1.2	4.2
Cladina and *Cladonia* spp.	41.6	29.2	31.9	32.2	40.9	32.4	38.8	40.7	38.4	56.5	55.6	33.9	32.7	42.6
Peltigera spp.	5.3	6.9	6.2	5.5	12.4	8.9	8.6	16.9	10.3	10.3	10.1	4.2	4.2	4.0
Nephroma spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Stereocaulon spp.	3.0	1.4	4.0	5.7	6.9	2.0	6.3	2.5	1.9	4.1	2.9	1.5	1.2	2.2
Unknown lichen	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carex spp.	4.2	6.9	3.2	5.7	1.1	4.4	4.0	1.2	5.0	4.9	2.3	5.3	5.3	4.1
Eriophorum spp.	0.0	0.0	0.0	0.5	1.1	0.6	1.1	1.2	0.4	0.0	0.0	0.9	1.1	3.8
Juncus and *Luzula* spp.	0.8	0.0	1.5	0.0	0.0	0.6	1.1	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Kobresia spp.	0.8	0.2	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arctagrostis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.7	1.0	0.0	0.0	0.0	0.0	0.0
Calamagrostis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.7	1.0	0.5	0.0	0.0	0.0	0.6
Poa spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Unknown grass	0.6	0.0	1.2	1.0	1.0	3.3	0.7	0.5	1.9	0.2	1.5	0.0	2.1	0.0
Allium spp.	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arenaria spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0
Equisetum spp.	0.0	0.0	1.0	0.0	0.6	1.3	1.4	5.1	1.2	6.1	10.6	1.3	0.0	0.0
Lupinus and *Oxytropis* spp.	0.0	0.0	0.0	0.0	0.0	1.3	1.4	0.2	0.0	0.4	0.0	0.0	0.0	0.0
Mustard	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown forb	0.0	0.0	0.2	0.0	0.6	0.0	0.4	0.8	0.0	0.0	0.0	0.0	0.2	0.4
Andromeda and *Cassiope* spp.	0.0	0.0	0.0	1.6	1.6	1.2	1.3	0.0	1.0	0.4	0.0	1.1	5.3	3.2
Arctostaphylos spp.	0.0	1.2	0.0	0.0	1.6	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0

Table E.3. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups (site) of caribou in the Western Arctic Herd in northwest Alaska, late winter, 2006-2008 (pgs. 215-216).

Year	2006					2007						2008		
Site no.	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Fecal samples per site	23	24	23	19	19	20	20	20	20	10	10	20	20	18
Betula spp.	1.9	1.2	1.3	1.6	0.0	1.2	0.0	0.9	1.0	0.0	0.0	5.3	0.0	0.0
Dryas spp.	0.0	0.0	0.0	0.0	1.6	2.3	1.3	0.9	0.0	0.0	1.0	0.0	1.3	0.0
Empetrum spp.	5.7	8.1	5.0	1.6	1.6	3.5	1.3	0.9	2.1	0.0	1.0	7.8	1.3	0.9
Ledum spp.	0.0	1.2	0.7	0.0	1.6	1.2	0.0	0.9	0.0	0.0	1.0	3.1	1.3	0.9
Salix spp.	3.5	3.6	4.8	3.1	1.6	1.2	1.3	1.9	2.1	0.4	1.0	2.2	2.6	3.2
Vaccinium spp.	5.1	5.3	3.2	1.6	1.6	2.3	2.5	0.9	1.0	0.4	1.0	4.2	1.3	3.4
Ericaceae spp.	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Unknown shrub	0.2	0.5	0.4	0.2	0.6	0.4	0.0	0.0	0.6	0.4	0.8	0.0	0.7	0.8
Picea spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7	0.0	0.8

Table E.4. Percent of plant fragments (not corrected for apparent digestibility) in composited fecal samples from groups (site) of caribou in the Chisana Herd in Alaska and Yukon Territory, late winter, 2006 and 2008.

Year	2006					2008		
Site no.	27	28	29	30	31	33	34	35
Fecal samples per site	5	5	5	5	5	10	10	10
Total moss	31.8	36.0	30.2	30.9	22.8	42.8	43.5	40.1
Cetraria and *Dactylina* spp.	0.0	0.0	0.0	0.0	0.0	8.5	10.7	11.4
Cladina and *Cladonia* spp.	45.8	37.2	39.1	21.0	42.5	27.1	31.5	23.1
Peltigera spp.	9.1	9.2	14.5	19.6	16.5	10.6	4.7	5.7
Stereocaulon spp.	0.8	0.7	1.2	0.9	1.1	1.3	1.9	0.6
Total sedge and rush	2.7	2.0	0.1	6.7	0.0	3.9	2.9	1.3
Total grasses	1.3	0.8	0.5	1.8	0.9	1.0	0.0	1.0
Equisetum spp.	0.0	1.4	1.1	5.9	3.5	0.4	0.6	0.0
Lupinus and *Oxytropis* spp.	1.0	1.9	0.5	0.0	0.4	0.0	0.0	12.7
Petasites spp.	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Saxifraga spp.	1.0	1.9	0.0	0.0	0.4	0.0	0.0	0.0
Unknown forb	1.3	1.0	0.3	0.5	0.8	0.4	0.1	0.0
Andromeda and *Cassiope* spp.	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0
Arctostaphylos spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Betula spp.	0.0	1.2	0.0	0.0	0.6	0.0	0.6	0.6
Dryas spp.	0.8	1.2	1.1	1.7	1.3	0.0	0.0	0.0
Empetrum spp.	0.8	1.2	6.4	0.8	6.7	0.0	0.0	0.6
Ledum spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Salix spp.	0.8	2.4	1.1	7.4	0.6	1.5	0.6	0.6
Vaccinium spp.	1.6	1.2	3.4	1.7	0.6	0.8	0.6	0.6
Unknown shrub	1.1	0.8	0.6	0.7	1.3	1.0	1.3	1.0
Picea spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2

Table E.5. Percent of plant fragments in composited fecal samples from groups (site) of caribou in the Denali Herd in central Alaska, late winter, 2007-2008.

Year	2007		2008	
Site no.	36	37	38	39
Fecal samples per site	15	15	15	15
Total moss	33.2	33.3	31.0	28.7
Alectoria and *Bryoria* spp.	1.0	0.0	0.0	4.3
Cetraria and *Dactylina* spp.	4.5	2.0	3.3	8.2
Cladina and *Cladonia* spp.	31.1	23.7	39.1	29.8
Peltigera spp.	5.4	4.1	17.2	9.4
Stereocaulon spp.	1.0	2.0	4.2	2.7
Carex spp.	10.4	9.1	0.0	3.2
Eriophorum spp.	2.0	6.5	0.0	0.7
Juncus and *Luzula* spp.	0.0	0.0	1.1	0.7
Arctagrostis spp.	0.5	0.5	0.0	1.1
Arctophila spp.	0.0	0.5	0.0	0.0
Bromus spp.	0.0	0.0	0.0	0.0
Calamagrostis spp.	0.0	0.5	0.4	1.1
Poa spp.	0.0	0.0	0.0	1.1
Unknown grass	0.5	0.8	0.0	1.2
Equisetum spp.	0.0	0.0	0.0	0.3
Lupinus and *Oxytropis* spp.	0.0	0.0	0.0	0.3
Polygonum spp.	0.0	0.0	0.4	0.0
Unknown forb	0.2	0.4	0.2	0.0
Andromeda and *Cassiope* spp.	1.3	3.3	0.0	0.9
Arctostaphylos spp.	0.0	0.0	0.0	0.9
Betula spp.	0.0	1.4	0.5	0.0
Empetrum spp.	2.7	1.4	0.0	0.0
Ledum spp.	1.3	1.4	0.5	0.9
Salix spp.	1.3	2.8	0.0	1.8
Vaccinium spp.	2.7	5.7	0.5	1.8
Unknown shrub	0.9	0.6	0.4	1.0
Picea spp.	0.0	0.0	1.1	0.0

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2006	2	-2.68	0.15	2.83	0.59	0.89	1.50
CAH	2006	2	0.16	-0.04	-0.20	1.15	1.59	2.83
CAH	2006	2	-3.09	2.48	5.57	0.37	0.52	0.69
CAH	2006	2	2.30	1.96	-0.34	1.18	1.42	1.82
CAH	2006	2	1.39	1.33	-0.06	1.15	1.42	1.84
CAH	2006	2	-1.73	1.17	2.90	0.69	0.90	1.22
CAH	2006	2	-1.57	1.09	2.66	0.68	0.94	1.26
CAH	2006	2	-3.20	1.74	4.94	0.38	0.57	0.82
CAH	2006	2	2.44	2.16	-0.28	1.17	1.40	1.72
CAH	2006	2	4.35	0.66	-3.70	1.71	2.21	3.14
CAH	2006	3	-1.16	1.31	2.48	0.76	0.98	1.28
CAH	2006	3	-1.25	0.44	1.69	0.82	1.10	1.50
CAH	2006	3	0.78	0.21	-0.58	1.17	1.51	2.05
CAH	2006	3	4.91	1.53	-3.39	1.54	1.81	2.24
CAH	2006	3	1.87	-2.94	-4.81	1.96	3.72	36.10
CAH	2006	3	-1.84	-0.13	1.71	0.79	1.11	1.72
CAH	2006	4	-5.03	1.19	6.22	0.19	0.42	0.61
CAH	2006	4	0.79	-0.23	-1.01	1.24	1.64	2.33
CAH	2006	4	-3.68	2.43	6.11	0.37	0.53	0.69
CAH	2006	4	-2.65	0.13	2.77	0.68	0.92	1.29
CAH	2006	4	-4.47	1.83	6.30	0.29	0.46	0.62
CAH	2006	4	-1.73	2.34	4.07	0.63	0.78	0.92
CAH	2006	4	-0.08	0.85	0.92	0.97	1.22	1.60

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2006	4	-1.27	0.62	1.89	0.82	1.08	1.43
CAH	2006	4	-4.16	1.80	5.96	0.33	0.50	0.70
CAH	2006	4	-0.51	-0.75	-0.25	1.08	1.54	2.75
CAH	2006	4	-2.48	0.90	3.38	0.60	0.83	1.10
CAH	2006	4	-2.87	2.49	5.36	0.49	0.62	0.77
CAH	2006	4	-5.79	0.62	6.40	0.11	0.34	0.60
CAH	2006	4	-2.00	-1.22	0.78	0.87	1.37	2.43
CAH	2006	4	-2.23	1.67	3.90	0.59	0.78	0.97
CAH	2006	4	-4.44	0.36	4.79	0.37	0.58	0.85
CAH	2007	5	-3.70	3.59	7.30	0.36	0.47	0.59
CAH	2007	5	-6.25	2.45	8.70	0.07	0.22	0.37
CAH	2007	5	-4.50	-0.24	4.26	0.40	0.65	0.94
CAH	2007	5	-3.09	1.23	4.32	0.53	0.71	0.93
CAH	2007	5	-2.58	1.27	3.84	0.57	0.78	1.01
CAH	2007	5	-6.03	0.47	6.50	0.12	0.33	0.53
CAH	2007	5	-3.20	0.85	4.05	0.54	0.74	1.03
CAH	2007	5	-2.35	-0.46	1.89	0.76	1.08	1.61
CAH	2007	5	-6.31	-0.42	5.89	0.10	0.32	0.62
CAH	2007	5	-3.41	0.17	3.57	0.56	0.79	1.15
CAH	2007	5	-4.24	2.10	6.34	0.30	0.49	0.65
CAH	2007	5	-2.58	1.24	3.82	0.60	0.79	1.01
CAH	2007	5	-1.46	0.19	1.64	0.86	1.12	1.51
CAH	2007	5	-3.59	1.28	4.87	0.47	0.64	0.81

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2007	5	-5.04	0.15	5.20	0.32	0.51	0.77
CAH	2007	6	-0.99	2.57	3.56	0.71	0.84	1.00
CAH	2007	6	-6.78	-2.14	4.64	-0.38	0.25	0.96
CAH	2007	6	-4.24	0.82	5.06	0.30	0.55	0.79
CAH	2007	6	-5.72	0.74	6.46	0.09	0.30	0.53
CAH	2007	6	-4.84	0.44	5.28	0.26	0.48	0.79
CAH	2007	6	-2.64	0.21	2.85	0.63	0.91	1.39
CAH	2007	6	-0.13	-0.71	-0.57	1.17	1.65	2.78
CAH	2007	6	-3.47	-0.96	2.51	0.60	0.96	1.63
CAH	2007	6	0.90	-0.93	-1.83	1.36	1.98	3.38
CAH	2007	6	-5.63	0.49	6.12	0.10	0.34	0.58
CAH	2007	6	-5.39	-0.62	4.77	0.20	0.47	0.89
CAH	2007	6	-6.92	0.96	7.89	-0.11	0.10	0.32
CAH	2007	6	-3.38	2.27	5.65	0.40	0.56	0.71
CAH	2007	6	-3.99	1.58	5.57	0.32	0.52	0.71
CAH	2007	6	-5.91	1.27	7.18	0.02	0.25	0.45
CAH	2007	6	-5.35	1.16	6.51	0.16	0.34	0.53
CAH	2007	6	-3.09	2.10	5.19	0.44	0.61	0.77
CAH	2007	7	-1.77	0.45	2.22	0.54	1.05	2.48
CAH	2007	7	-1.37	2.13	3.50	0.44	0.71	1.04
CAH	2007	7	-2.38	0.24	2.62	0.36	0.86	2.72
CAH	2007	8	-4.79	2.21	7.00	0.10	0.29	0.48
CAH	2007	8	-1.95	-0.54	1.41	0.83	1.24	2.28

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2007	8	-5.78	1.34	7.12	-0.10	0.16	0.40
CAH	2007	8	-4.45	1.14	5.59	0.19	0.41	0.65
CAH	2007	8	-3.79	1.65	5.44	0.26	0.48	0.69
CAH	2007	8	-2.69	2.00	4.68	0.45	0.63	0.84
CAH	2007	8	-3.24	2.27	5.51	0.35	0.52	0.70
CAH	2007	8	-2.58	1.95	4.53	0.48	0.65	0.86
CAH	2007	8	-4.95	0.76	5.70	0.05	0.34	0.66
CAH	2007	8	-5.26	0.30	5.55	-0.04	0.31	0.61
CAH	2007	8	-4.13	2.44	6.57	0.20	0.37	0.54
CAH	2007	8	-5.83	0.02	5.84	-0.15	0.20	0.49
CAH	2007	8	-5.75	1.33	7.07	-0.15	0.16	0.35
CAH	2007	8	-4.82	2.18	7.00	0.08	0.29	0.48
CAH	2007	8	-4.99	1.83	6.83	0.03	0.27	0.44
CAH	2007	9	1.46	1.63	0.17	1.09	1.35	1.75
CAH	2007	9	-1.27	0.88	2.15	0.77	1.03	1.42
CAH	2007	9	0.01	0.37	0.36	1.03	1.39	2.06
CAH	2007	9	-2.73	-1.11	1.62	0.75	1.21	2.43
CAH	2007	9	1.75	-0.68	-2.43	1.49	2.22	4.06
CAH	2007	9	-4.70	1.30	6.00	0.16	0.38	0.62
CAH	2007	9	-1.25	1.65	2.89	0.67	0.91	1.16
CAH	2007	9	-0.62	1.11	1.72	0.86	1.11	1.50
CAH	2007	9	0.07	1.18	1.11	0.94	1.21	1.57
CAH	2007	9	-2.31	1.43	3.74	0.56	0.77	1.02

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2007	9	-0.17	0.54	0.71	1.02	1.32	1.92
CAH	2007	9	-2.85	0.38	3.23	0.56	0.82	1.17
CAH	2007	9	-0.33	2.30	2.64	0.78	0.95	1.16
CAH	2007	9	0.08	2.13	2.05	0.84	1.04	1.26
CAH	2007	9	3.61	-1.87	-5.48	2.23	3.86	13.75
CAH	2007	9	-2.90	1.10	4.00	0.49	0.70	0.97
CAH	2007	9	-5.22	1.08	6.30	0.06	0.30	0.50
CAH	2008	10	-6.10	1.68	7.78	-0.31	-0.01	0.21
CAH	2008	10	-6.71	1.62	8.33	-0.53	-0.11	0.12
CAH	2008	10	-3.07	2.77	5.84	0.27	0.46	0.62
CAH	2008	10	-3.43	1.47	4.91	0.16	0.51	0.78
CAH	2008	10	-1.26	2.80	4.06	0.56	0.74	0.94
CAH	2008	10	-2.57	3.69	6.25	0.32	0.48	0.62
CAH	2008	10	-1.45	3.58	5.03	0.49	0.63	0.78
CAH	2008	10	-3.92	2.92	6.84	0.10	0.33	0.50
CAH	2008	10	-3.19	3.10	6.28	0.24	0.43	0.60
CAH	2008	10	-3.14	3.53	6.67	0.20	0.40	0.58
CAH	2008	10	-3.52	0.73	4.25	0.28	0.58	0.92
CAH	2008	10	-2.24	2.57	4.81	0.44	0.61	0.81
CAH	2008	10	-4.19	3.87	8.06	0.04	0.25	0.40
CAH	2008	10	-1.96	2.73	4.69	0.43	0.64	0.83
CAH	2008	10	-3.49	2.24	5.74	0.22	0.43	0.65
CAH	2008	10	-2.38	1.82	4.20	0.43	0.66	0.92

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2008	10	-6.00	2.27	8.26	-0.29	0.01	0.24
CAH	2008	11	-5.46	2.49	7.96	0.16	0.30	0.45
CAH	2008	11	-7.96	2.57	10.53	-0.15	-0.01	0.14
CAH	2008	11	-1.96	2.12	4.08	0.63	0.77	0.94
CAH	2008	11	-2.62	2.91	5.53	0.52	0.63	0.75
CAH	2008	11	-5.37	0.34	5.71	0.24	0.43	0.63
CAH	2008	11	-6.74	1.97	8.71	-0.02	0.15	0.29
CAH	2008	11	-4.56	2.31	6.87	0.28	0.42	0.58
CAH	2008	11	-6.78	2.21	8.99	-0.01	0.14	0.27
CAH	2008	11	-8.43	1.18	9.61	-0.27	-0.08	0.09
CAH	2008	11	-8.27	1.64	9.91	-0.29	-0.06	0.12
CAH	2008	11	-6.95	0.56	7.51	-0.03	0.16	0.32
CAH	2008	11	-6.70	0.56	7.26	0.01	0.19	0.39
CAH	2008	11	-2.00	0.14	2.14	0.78	1.03	1.43
CAH	2008	11	-5.63	-0.28	5.35	0.24	0.43	0.80
CAH	2008	11	-6.27	-0.65	5.62	0.10	0.33	0.65
CAH	2008	11	-6.10	0.18	6.28	0.09	0.31	0.52
CAH	2008	11	-5.68	0.31	5.99	0.20	0.37	0.60
CAH	2008	11	-8.72	0.94	9.65	-0.33	-0.13	0.07
CAH	2008	12	-4.36	2.01	6.37	0.17	0.35	0.52
CAH	2008	12	-7.23	0.29	7.52	-0.59	-0.16	0.13
CAH	2008	12	-6.09	-0.13	5.96	-0.17	0.10	0.44
CAH	2008	12	-6.87	-0.29	6.58	-0.47	-0.09	0.22

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CAH	2008	12	-5.67	-0.08	5.59	-0.10	0.20	0.54
CAH	2008	12	-3.72	0.27	3.99	0.37	0.62	0.99
CAH	2008	12	-3.95	-0.61	3.34	0.35	0.72	1.38
CAH	2008	12	-5.06	-0.60	4.46	0.11	0.40	0.92
CAH	2008	12	-6.94	-2.57	4.36	-92.70	-0.27	365.82
WAH	2006	13	-9.27	3.50	12.77	-0.57	-0.33	-0.17
WAH	2006	13	-6.22	3.29	9.51	-0.10	0.06	0.22
WAH	2006	13	-6.73	4.26	10.98	-0.15	-0.01	0.13
WAH	2006	13	-9.08	3.00	12.08	-0.53	-0.33	-0.16
WAH	2006	13	-7.34	3.83	11.17	-0.24	-0.08	0.06
WAH	2006	13	-7.87	2.76	10.63	-0.38	-0.17	0.02
WAH	2006	13	-6.87	3.35	10.23	-0.21	-0.03	0.13
WAH	2006	13	-7.96	3.10	11.06	-0.45	-0.17	-0.01
WAH	2006	13	-7.92	3.02	10.93	-0.38	-0.17	-0.01
WAH	2006	13	-8.70	2.96	11.66	-0.48	-0.28	-0.11
WAH	2006	13	-7.52	2.37	9.90	-0.31	-0.13	0.05
WAH	2006	13	-7.49	3.56	11.05	-0.27	-0.10	0.04
WAH	2006	13	-8.52	3.32	11.84	-0.40	-0.24	-0.05
WAH	2006	13	-7.12	3.99	11.11	-0.22	-0.06	0.08
WAH	2006	13	-6.83	3.31	10.14	-0.19	-0.02	0.13
WAH	2006	13	-7.58	3.51	11.09	-0.30	-0.12	0.02
WAH	2006	13	-7.10	3.58	10.68	-0.23	-0.06	0.10
WAH	2006	13	-7.61	3.05	10.66	-0.38	-0.12	0.03

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2006	14	-7.81	3.37	11.18	-0.38	-0.15	0.07
WAH	2006	14	-8.06	2.68	10.73	-0.46	-0.20	-0.02
WAH	2006	14	-7.79	3.60	11.39	-0.38	-0.14	0.01
WAH	2006	14	-6.70	3.06	9.76	-0.19	0.00	0.16
WAH	2006	14	-7.57	3.26	10.83	-0.30	-0.12	0.06
WAH	2006	14	-5.97	3.52	9.49	-0.09	0.09	0.23
WAH	2006	14	-4.95	3.86	8.81	0.06	0.21	0.35
WAH	2006	14	-7.23	2.93	10.17	-0.32	-0.08	0.13
WAH	2006	14	-6.18	3.62	9.81	-0.11	0.06	0.23
WAH	2006	14	-9.02	3.31	12.33	-0.56	-0.31	-0.12
WAH	2006	14	-7.23	4.10	11.32	-0.27	-0.07	0.11
WAH	2006	14	-9.19	2.56	11.75	-0.63	-0.37	-0.15
WAH	2006	14	-8.88	2.95	11.83	-0.55	-0.30	-0.09
WAH	2006	14	-7.37	3.03	10.40	-0.28	-0.10	0.05
WAH	2006	14	-7.65	3.13	10.78	-0.31	-0.13	0.04
WAH	2006	14	-7.85	2.78	10.62	-0.40	-0.17	0.02
WAH	2006	15	-6.08	3.08	9.15	-0.07	0.13	0.30
WAH	2006	15	-6.04	2.41	8.45	-0.04	0.15	0.33
WAH	2006	15	-9.05	2.85	11.90	-0.48	-0.26	-0.08
WAH	2006	15	-6.13	3.17	9.30	-0.06	0.13	0.29
WAH	2006	15	-6.24	3.35	9.58	-0.10	0.11	0.26
WAH	2006	15	-5.25	3.83	9.08	0.03	0.22	0.36
WAH	2006	15	-5.86	3.67	9.53	-0.03	0.15	0.31

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2006	15	-6.16	3.53	9.70	-0.05	0.11	0.25
WAH	2006	15	-7.29	2.73	10.02	-0.21	-0.02	0.15
WAH	2006	15	-7.20	3.22	10.42	-0.21	-0.01	0.16
WAH	2006	15	-4.18	3.00	7.18	0.21	0.38	0.51
WAH	2006	15	-6.47	2.85	9.32	-0.11	0.08	0.25
WAH	2006	15	-5.94	2.65	8.58	-0.07	0.16	0.35
WAH	2006	15	-3.90	3.71	7.62	0.21	0.38	0.52
WAH	2006	15	-6.66	3.62	10.28	-0.12	0.05	0.20
WAH	2006	15	-4.85	3.41	8.26	0.11	0.28	0.41
WAH	2006	15	-3.33	3.47	6.80	0.32	0.46	0.61
WAH	2006	16	-4.03	3.59	7.62	0.20	0.34	0.48
WAH	2006	16	-6.14	3.76	9.90	-0.13	0.07	0.20
WAH	2006	16	-3.16	3.63	6.79	0.31	0.45	0.57
WAH	2006	16	-6.07	4.14	10.20	-0.08	0.08	0.22
WAH	2006	16	-4.99	3.81	8.79	0.06	0.21	0.37
WAH	2006	16	-6.28	3.19	9.47	-0.10	0.06	0.21
WAH	2006	16	-5.74	3.73	9.46	-0.05	0.12	0.25
WAH	2006	16	-3.38	3.60	6.98	0.28	0.42	0.54
WAH	2006	16	-6.57	3.72	10.28	-0.13	0.02	0.17
WAH	2006	16	-0.90	3.07	3.97	0.65	0.78	0.93
WAH	2006	16	-3.44	4.15	7.59	0.27	0.38	0.49
WAH	2006	16	-4.89	4.05	8.94	0.06	0.22	0.35
WAH	2006	16	-6.78	3.69	10.48	-0.20	-0.01	0.15

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2006	16	-4.25	3.53	7.78	0.18	0.31	0.45
WAH	2006	16	-6.91	4.09	11.00	-0.23	-0.02	0.11
WAH	2006	16	-5.17	3.51	8.69	-0.01	0.19	0.34
WAH	2006	16	-2.65	3.71	6.36	0.38	0.50	0.63
WAH	2006	16	-2.57	4.12	6.69	0.38	0.49	0.63
WAH	2006	16	-2.57	3.75	6.32	0.37	0.51	0.62
WAH	2006	17	-1.82	2.34	4.16	0.58	0.74	0.91
WAH	2006	17	-0.39	2.87	3.26	0.74	0.88	1.04
WAH	2006	17	-1.92	3.59	5.52	0.48	0.61	0.74
WAH	2006	17	1.73	2.88	1.15	1.00	1.16	1.35
WAH	2006	17	0.71	3.21	2.50	0.83	0.98	1.13
WAH	2006	17	-3.65	3.28	6.93	0.28	0.42	0.55
WAH	2006	17	-0.03	4.07	4.10	0.69	0.80	0.91
WAH	2006	17	-4.72	2.81	7.53	0.13	0.30	0.46
WAH	2006	17	-2.54	3.44	5.98	0.43	0.55	0.68
WAH	2006	17	-2.58	2.87	5.45	0.46	0.59	0.73
WAH	2006	17	-2.69	3.88	6.56	0.38	0.50	0.62
WAH	2006	17	-1.67	3.37	5.04	0.54	0.66	0.79
WAH	2006	17	-6.22	3.10	9.32	-0.05	0.10	0.22
WAH	2006	17	-6.32	2.62	8.94	-0.07	0.09	0.25
WAH	2006	17	-1.29	3.30	4.59	0.60	0.72	0.86
WAH	2006	17	-3.05	3.75	6.80	0.36	0.47	0.58
WAH	2006	17	-1.78	3.44	5.22	0.49	0.65	0.77

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2006	17	-3.68	3.20	6.88	0.29	0.42	0.56
WAH	2007	18	-7.88	2.48	10.36	-0.32	-0.11	0.08
WAH	2007	18	-8.36	1.33	9.69	-0.59	-0.21	0.01
WAH	2007	18	-6.75	2.43	9.18	-0.18	0.05	0.22
WAH	2007	18	-8.55	1.46	10.00	-0.49	-0.24	0.00
WAH	2007	18	-6.85	1.33	8.17	-0.18	0.04	0.24
WAH	2007	18	-8.56	1.44	10.00	-0.53	-0.24	0.05
WAH	2007	18	-6.77	2.77	9.54	-0.17	0.04	0.23
WAH	2007	18	-6.72	3.04	9.75	-0.17	0.05	0.22
WAH	2007	18	-9.26	2.80	12.06	-0.52	-0.29	-0.11
WAH	2007	19	-6.92	2.70	9.62	-0.34	-0.07	0.14
WAH	2007	19	-7.18	-0.39	6.79	-0.91	-0.19	0.13
WAH	2007	19	-7.86	1.73	9.59	-0.61	-0.24	0.02
WAH	2007	19	-8.04	0.24	8.28	-1.09	-0.37	0.01
WAH	2007	19	-8.52	1.74	10.26	-0.76	-0.36	-0.09
WAH	2007	19	-8.61	0.90	9.50	-0.96	-0.43	-0.11
WAH	2007	21	-7.65	2.51	10.16	-0.63	-0.22	0.08
WAH	2007	21	-7.98	2.33	10.31	-0.75	-0.28	-0.01
WAH	2007	21	-5.72	1.44	7.16	-0.26	0.09	0.34
WAH	2007	21	-7.91	0.36	8.27	-1.95	-0.39	0.00
WAH	2007	21	-9.16	0.87	10.03	-1.41	-0.61	-0.20
WAH	2007	21	-6.00	3.13	9.12	-0.32	0.03	0.27
WAH	2008	24	-7.80	3.92	11.72	-0.62	-0.33	-0.13

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2008	24	-8.25	4.18	12.42	-0.62	-0.38	-0.19
WAH	2008	24	-4.86	3.70	8.56	-0.10	0.09	0.23
WAH	2008	24	-6.55	2.14	8.69	-0.53	-0.21	0.00
WAH	2008	24	-6.81	3.08	9.89	-0.48	-0.22	-0.03
WAH	2008	24	-2.32	4.07	6.39	0.25	0.44	0.58
WAH	2008	24	-6.32	4.23	10.55	-0.29	-0.12	0.02
WAH	2008	24	-5.75	3.96	9.71	-0.25	-0.04	0.14
WAH	2008	24	-4.26	4.14	8.40	-0.02	0.17	0.33
WAH	2008	24	-7.06	3.46	10.52	-0.51	-0.24	-0.06
WAH	2008	24	-7.86	2.97	10.83	-0.68	-0.39	-0.18
WAH	2008	24	-6.31	3.88	10.19	-0.32	-0.12	0.04
WAH	2008	24	-3.16	3.64	6.80	0.19	0.34	0.51
WAH	2008	24	-5.35	4.73	10.08	-0.18	0.01	0.15
WAH	2008	24	-8.17	3.74	11.90	-0.64	-0.39	-0.19
WAH	2008	24	-5.28	3.67	8.95	-0.14	0.02	0.20
WAH	2008	24	-5.06	4.58	9.64	-0.12	0.05	0.20
WAH	2008	24	-6.79	1.33	8.13	-0.71	-0.30	-0.03
WAH	2008	24	-5.16	3.09	8.24	-0.16	0.05	0.21
WAH	2008	25	-8.76	5.35	14.10	-0.45	-0.28	-0.13
WAH	2008	25	-8.78	4.55	13.33	-0.50	-0.31	-0.13
WAH	2008	25	-6.05	3.58	9.63	-0.21	0.02	0.16
WAH	2008	25	-4.54	3.61	8.15	0.07	0.22	0.35
WAH	2008	25	-6.29	3.57	9.86	-0.18	-0.02	0.15

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2008	25	-5.08	4.01	9.10	-0.04	0.14	0.28
WAH	2008	25	-5.61	4.66	10.27	-0.09	0.07	0.19
WAH	2008	25	-5.69	4.64	10.33	-0.12	0.06	0.19
WAH	2008	25	-4.43	4.05	8.48	0.04	0.22	0.34
WAH	2008	25	-6.00	3.88	9.88	-0.14	0.02	0.16
WAH	2008	25	-4.46	3.27	7.72	0.02	0.24	0.38
WAH	2008	25	-5.83	4.40	10.24	-0.10	0.04	0.19
WAH	2008	25	-7.53	4.04	11.58	-0.35	-0.17	-0.03
WAH	2008	25	-5.39	4.53	9.93	-0.06	0.09	0.22
WAH	2008	25	-5.01	4.82	9.83	0.01	0.13	0.25
WAH	2008	25	-6.68	4.43	11.11	-0.20	-0.06	0.07
WAH	2008	25	-8.55	3.85	12.40	-0.50	-0.31	-0.12
WAH	2008	25	-6.12	4.31	10.43	-0.14	0.01	0.15
WAH	2008	25	-3.21	4.00	7.21	0.24	0.38	0.50
WAH	2008	26	-5.88	3.67	9.55	-0.11	0.08	0.25
WAH	2008	26	-6.05	4.06	10.11	-0.14	0.05	0.18
WAH	2008	26	-6.61	4.07	10.68	-0.20	-0.02	0.15
WAH	2008	26	-4.64	4.52	9.16	0.06	0.21	0.35
WAH	2008	26	-5.52	3.99	9.51	-0.06	0.12	0.27
WAH	2008	26	-4.42	4.15	8.57	0.10	0.25	0.39
WAH	2008	26	-2.74	5.67	8.40	0.24	0.38	0.50
WAH	2008	26	-8.20	4.84	13.04	-0.37	-0.20	-0.04
WAH	2008	26	-6.54	5.08	11.62	-0.21	-0.01	0.12

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
WAH	2008	26	-8.15	4.11	12.26	-0.44	-0.21	-0.05
WAH	2008	26	-4.43	5.38	9.81	0.06	0.21	0.35
WAH	2008	26	-7.69	3.95	11.64	-0.40	-0.16	0.05
WAH	2008	26	-7.12	3.04	10.16	-0.32	-0.09	0.11
WAH	2008	26	-5.59	4.11	9.69	-0.07	0.11	0.26
WAH	2008	26	-6.76	3.90	10.66	-0.26	-0.04	0.15
WAH	2008	26	-4.88	5.40	10.27	0.01	0.17	0.30
WAH	2008	26	-7.45	4.45	11.90	-0.32	-0.12	0.04
WAH	2008	26	-2.11	4.09	6.20	0.41	0.53	0.65
WAH	2008	26	-5.82	3.85	9.67	-0.10	0.08	0.22
WAH	2008	26	-5.67	3.68	9.35	-0.09	0.10	0.26
CH	2006	27	-4.19	3.67	7.86	0.24	0.37	0.50
CH	2006	27	-2.54	2.45	4.98	0.48	0.65	0.81
CH	2006	28	-4.34	3.23	7.57	0.26	0.37	0.52
CH	2006	28	-4.61	3.58	8.19	0.15	0.31	0.42
CH	2006	28	-2.89	3.66	6.55	0.36	0.51	0.61
CH	2006	29	-6.00	2.84	8.84	-0.04	0.17	0.31
CH	2006	29	-4.64	2.19	6.83	0.20	0.39	0.57
CH	2006	29	-4.20	3.61	7.81	0.19	0.38	0.49
CH	2006	29	-3.75	2.44	6.19	0.34	0.50	0.65
CH	2006	30	-4.06	2.99	7.05	-0.02	0.22	0.40
CH	2006	30	-2.61	3.22	5.83	0.26	0.44	0.64
CH	2006	30	-0.91	2.91	3.82	0.56	0.75	0.96

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
CH	2006	30	-4.32	2.41	6.73	-0.05	0.20	0.44
CH	2006	31	-4.87	2.15	7.02	0.21	0.34	0.49
CH	2006	31	-4.67	2.20	6.87	0.23	0.39	0.57
CH	2006	31	-2.66	2.63	5.29	0.50	0.63	0.76
CH	2006	31	-5.08	2.68	7.76	0.18	0.32	0.48
CH	2006	32	-4.04	1.89	5.93	0.01	0.31	0.54
CH	2006	32	-4.14	2.88	7.02	0.01	0.25	0.49
CH	2008	33	-0.83	0.71	1.54	0.82	1.19	1.87
CH	2008	33	-1.95	2.82	4.77	0.45	0.63	0.79
CH	2008	33	-1.21	3.04	4.25	0.57	0.72	0.91
CH	2008	33	-1.39	1.89	3.28	0.59	0.84	1.11
CH	2008	34	3.34	1.61	-1.73	1.38	1.70	2.15
CH	2008	34	-1.39	2.93	4.33	0.57	0.73	0.87
CH	2008	34	-1.62	2.38	4.00	0.57	0.75	0.98
CH	2008	35	-1.19	-1.28	-0.09	1.14	2.18	31.01
CH	2008	35	-0.42	2.09	2.51	0.75	0.97	1.26
DH	2007	36	-4.81	2.12	6.92	0.09	0.28	0.46
DH	2007	36	-4.99	0.60	5.58	0.07	0.33	0.57
DH	2007	36	-5.55	2.45	8.00	-0.02	0.15	0.31
DH	2007	36	-7.05	1.15	8.19	-0.32	-0.09	0.10
DH	2007	36	-5.54	1.45	6.98	-0.02	0.18	0.38
DH	2007	36	-4.15	2.45	6.60	0.19	0.36	0.53
DH	2007	36	-7.42	1.90	9.32	-0.40	-0.14	0.03

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
DH	2007	36	-2.89	1.94	4.83	0.43	0.60	0.80
DH	2007	36	-7.66	1.53	9.18	-0.44	-0.19	0.04
DH	2007	36	-4.78	1.38	6.16	0.15	0.32	0.51
DH	2007	36	-8.27	2.91	11.17	-0.47	-0.24	-0.07
DH	2007	36	-5.73	2.70	8.43	-0.05	0.12	0.29
DH	2007	36	-6.66	2.33	9.00	-0.23	-0.02	0.18
DH	2007	37	-6.09	2.96	9.06	-0.27	-0.03	0.19
DH	2007	37	-4.71	2.86	7.57	-0.17	0.19	0.35
DH	2007	37	-6.57	2.27	8.84	-0.46	-0.12	0.10
DH	2007	37	-4.55	1.94	6.49	-0.03	0.24	0.47
DH	2007	37	-5.31	1.79	7.10	-0.18	0.10	0.34
DH	2007	37	-5.45	2.40	7.85	-0.19	0.07	0.32
DH	2007	37	-6.46	1.96	8.41	-0.53	-0.11	0.13
DH	2007	37	-5.03	2.14	7.16	-0.20	0.15	0.34
DH	2007	37	-6.62	1.14	7.76	-0.80	-0.17	0.16
DH	2007	37	-7.13	0.90	8.03	-0.85	-0.28	0.02
DH	2007	37	-4.42	2.37	6.80	-0.02	0.24	0.46
DH	2007	37	-9.44	2.85	12.29	-0.94	-0.57	-0.28
DH	2008	38	-3.57	3.51	7.08	0.06	0.24	0.44
DH	2008	38	-6.53	4.54	11.07	-0.41	-0.20	-0.04
DH	2008	38	-2.44	4.84	7.28	0.19	0.34	0.46
DH	2008	38	-5.64	4.02	9.65	-0.29	-0.08	0.07
DH	2008	38	-5.62	3.15	8.77	-0.38	-0.10	0.10

Table E.6. The isotopic ratios of $^{15}N/^{14}N$ (δ) in urea and body N (as isolated from urines in snow, $n = 379$) and the simulated values of the proportion of urea N derived from body N (p-UN) for caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali (DH) caribou herds, late winter, 2006-2008 (pgs. 219-235).

Population	Year	Site no.	$\delta^{15}N$		$\Delta_{Body\text{-}urea}$	p-UN		
			Urea	Body		Minimum	Median	Maximum
DH	2008	39	-4.88	3.71	8.59	-0.04	0.18	0.33
DH	2008	39	-5.41	4.02	9.43	-0.15	0.11	0.29
DH	2008	39	-5.01	2.91	7.92	-0.08	0.19	0.40
DH	2008	39	-4.80	2.18	6.98	-0.03	0.24	0.49
DH	2008	39	-6.31	1.87	8.17	-0.41	-0.01	0.29
DH	2008	39	-4.68	2.26	6.93	-0.04	0.26	0.47
DH	2008	39	-6.90	3.65	10.55	-0.34	-0.08	0.12
DH	2008	39	-5.68	4.10	9.77	-0.14	0.08	0.27
DH	2008	39	-5.01	4.42	9.43	-0.08	0.15	0.30
DH	2008	39	-2.39	3.12	5.51	0.38	0.55	0.69
DH	2008	39	-6.76	3.69	10.45	-0.30	-0.06	0.13

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CAH	2006	1	-2.27
CAH	2006	1	-2.16
CAH	2006	1	-2.07
CAH	2006	1	-1.51
CAH	2006	1	-1.45
CAH	2006	1	-1.34
CAH	2006	1	-1.20
CAH	2006	1	-1.16
CAH	2006	1	-1.13
CAH	2006	1	-1.08
CAH	2006	1	-1.08
CAH	2006	1	-0.96
CAH	2006	1	-0.92
CAH	2006	1	-0.88
CAH	2006	1	-0.82
CAH	2006	1	-0.70
CAH	2006	1	-0.67
CAH	2006	1	-0.67
CAH	2006	1	-0.63
CAH	2006	1	-0.50
CAH	2006	1	-0.33
CAH	2006	2	-1.49
CAH	2006	2	-1.37
CAH	2006	2	-1.18
CAH	2006	2	-1.13
CAH	2006	2	-1.12
CAH	2006	2	-0.96
CAH	2006	2	-0.93
CAH	2006	2	-0.92
CAH	2006	2	-0.76
CAH	2006	2	-0.67
CAH	2006	2	-0.62
CAH	2006	2	-0.59
CAH	2006	2	-0.43
CAH	2006	2	-0.39
CAH	2006	2	-0.37

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CAH	2006	2	-0.25
CAH	2006	2	-0.11
CAH	2006	2	0.02
CAH	2006	3	-2.94
CAH	2006	3	-2.88
CAH	2006	3	-2.75
CAH	2006	3	-2.75
CAH	2006	3	-2.64
CAH	2006	3	-2.61
CAH	2006	3	-2.40
CAH	2006	3	-2.37
CAH	2006	3	-2.37
CAH	2006	3	-2.32
CAH	2006	3	-2.16
CAH	2006	3	-2.05
CAH	2006	3	-2.02
CAH	2006	3	-1.96
CAH	2006	3	-1.94
CAH	2006	3	-1.84
CAH	2006	3	-1.68
CAH	2006	3	-1.59
CAH	2006	3	-1.26
CAH	2006	3	-1.12
CAH	2006	4	-2.58
CAH	2006	4	-2.35
CAH	2006	4	-2.33
CAH	2006	4	-2.12
CAH	2006	4	-1.99
CAH	2006	4	-1.42
CAH	2007	5	-3.06
CAH	2007	5	-2.78
CAH	2007	5	-2.47
CAH	2007	5	-2.44
CAH	2007	5	-2.28
CAH	2007	5	-2.28
CAH	2007	5	-2.21

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CAH	2007	5	-2.19
CAH	2007	5	-1.84
CAH	2007	5	-1.76
CAH	2007	6	-2.61
CAH	2007	6	-2.57
CAH	2007	6	-2.43
CAH	2007	6	-2.14
CAH	2007	6	-2.06
CAH	2007	6	-2.02
CAH	2007	6	-1.99
CAH	2007	6	-1.98
CAH	2007	6	-1.92
CAH	2007	6	-1.81
CAH	2007	6	-1.76
CAH	2007	6	-1.72
CAH	2007	6	-1.62
CAH	2007	6	-1.46
CAH	2007	6	-1.43
CAH	2007	6	-1.40
CAH	2007	6	-1.16
CAH	2007	6	-1.02
CAH	2007	7	0.93
CAH	2007	7	1.16
CAH	2007	7	1.20
CAH	2007	7	1.20
CAH	2007	7	1.21
CAH	2007	7	1.28
CAH	2007	7	1.43
CAH	2007	7	1.46
CAH	2007	7	1.48
CAH	2007	7	1.49
CAH	2007	7	1.59
CAH	2007	7	1.62
CAH	2007	7	1.64
CAH	2007	7	1.65
CAH	2007	7	1.72

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CAH	2007	7	1.74
CAH	2007	7	1.77
CAH	2007	7	1.80
CAH	2007	7	1.82
CAH	2007	7	1.84
CAH	2007	9	-2.15
CAH	2007	9	-2.05
CAH	2007	9	-1.93
CAH	2007	9	-1.92
CAH	2007	9	-1.65
CAH	2007	9	-1.51
CAH	2007	9	-1.42
CAH	2007	9	-1.37
CAH	2007	9	-1.30
CAH	2007	9	-1.11
CAH	2007	9	-1.09
CAH	2007	9	-1.06
CAH	2007	9	-0.91
CAH	2007	9	-0.90
CAH	2007	9	-0.86
CAH	2007	9	-0.85
CAH	2007	9	-0.79
CAH	2007	9	-0.71
CAH	2007	9	-0.51
CAH	2007	9	-0.47
CAH	2008	10	-1.26
CAH	2008	10	-1.17
CAH	2008	10	-0.97
CAH	2008	10	-0.84
CAH	2008	10	-0.78
CAH	2008	10	-0.77
CAH	2008	10	-0.72
CAH	2008	10	-0.71
CAH	2008	10	-0.62
CAH	2008	10	-0.27
CAH	2008	10	-0.26

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CAH	2008	10	-0.16
CAH	2008	10	-0.04
CAH	2008	10	0.02
CAH	2008	10	0.11
CAH	2008	10	0.13
CAH	2008	10	0.15
CAH	2008	10	0.20
CAH	2008	10	0.21
CAH	2008	10	0.24
CAH	2008	11	-2.64
CAH	2008	11	-2.46
CAH	2008	11	-2.37
CAH	2008	11	-2.33
CAH	2008	11	-2.33
CAH	2008	11	-2.29
CAH	2008	11	-2.28
CAH	2008	11	-2.28
CAH	2008	11	-2.27
CAH	2008	11	-2.25
CAH	2008	11	-2.23
CAH	2008	11	-2.21
CAH	2008	11	-2.19
CAH	2008	11	-2.08
CAH	2008	11	-2.05
CAH	2008	11	-2.05
CAH	2008	11	-1.92
CAH	2008	11	-1.92
CAH	2008	11	-1.71
CAH	2008	11	-1.70
CAH	2008	12	-1.26
CAH	2008	12	-1.24
CAH	2008	12	-1.19
CAH	2008	12	-1.12
CAH	2008	12	-1.12
CAH	2008	12	-0.94
CAH	2008	12	-0.86

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CAH	2008	12	-0.85
CAH	2008	12	-0.85
CAH	2008	12	-0.85
CAH	2008	12	-0.76
CAH	2008	12	-0.69
CAH	2008	12	-0.66
CAH	2008	12	-0.66
CAH	2008	12	-0.65
CAH	2008	12	-0.58
CAH	2008	12	-0.57
CAH	2008	12	-0.43
CAH	2008	12	-0.39
CAH	2008	12	-0.36
WAH	2006	13	-1.44
WAH	2006	13	-1.34
WAH	2006	13	-1.32
WAH	2006	13	-1.29
WAH	2006	13	-1.25
WAH	2006	13	-1.20
WAH	2006	13	-1.19
WAH	2006	13	-1.12
WAH	2006	13	-1.09
WAH	2006	13	-1.07
WAH	2006	13	-1.06
WAH	2006	13	-1.05
WAH	2006	13	-1.00
WAH	2006	13	-0.99
WAH	2006	13	-0.98
WAH	2006	13	-0.95
WAH	2006	13	-0.94
WAH	2006	13	-0.91
WAH	2006	13	-0.69
WAH	2006	13	-0.69
WAH	2006	13	-0.57
WAH	2006	13	-0.47
WAH	2006	13	-0.36

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2006	14	-2.00
WAH	2006	14	-1.69
WAH	2006	14	-1.35
WAH	2006	14	-1.29
WAH	2006	14	-1.26
WAH	2006	14	-1.25
WAH	2006	14	-1.25
WAH	2006	14	-1.24
WAH	2006	14	-1.12
WAH	2006	14	-1.06
WAH	2006	14	-1.03
WAH	2006	14	-1.01
WAH	2006	14	-0.95
WAH	2006	14	-0.90
WAH	2006	14	-0.87
WAH	2006	14	-0.86
WAH	2006	14	-0.79
WAH	2006	14	-0.76
WAH	2006	14	-0.76
WAH	2006	14	-0.65
WAH	2006	14	-0.63
WAH	2006	14	-0.51
WAH	2006	14	-0.40
WAH	2006	14	-0.28
WAH	2006	15	-2.21
WAH	2006	15	-2.13
WAH	2006	15	-1.91
WAH	2006	15	-1.85
WAH	2006	15	-1.82
WAH	2006	15	-1.78
WAH	2006	15	-1.75
WAH	2006	15	-1.72
WAH	2006	15	-1.71
WAH	2006	15	-1.58
WAH	2006	15	-1.53
WAH	2006	15	-1.46

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2006	15	-1.43
WAH	2006	15	-1.41
WAH	2006	15	-1.37
WAH	2006	15	-1.29
WAH	2006	15	-1.22
WAH	2006	15	-1.19
WAH	2006	15	-1.13
WAH	2006	15	-0.90
WAH	2006	15	-0.86
WAH	2006	15	-0.44
WAH	2006	15	-0.32
WAH	2006	16	-1.80
WAH	2006	16	-1.62
WAH	2006	16	-1.53
WAH	2006	16	-1.39
WAH	2006	16	-1.39
WAH	2006	16	-1.22
WAH	2006	16	-1.19
WAH	2006	16	-1.15
WAH	2006	16	-1.10
WAH	2006	16	-1.01
WAH	2006	16	-0.91
WAH	2006	16	-0.85
WAH	2006	16	-0.84
WAH	2006	16	-0.81
WAH	2006	16	-0.80
WAH	2006	16	-0.69
WAH	2006	16	-0.69
WAH	2006	16	-0.66
WAH	2006	16	-0.39
WAH	2006	17	-1.82
WAH	2006	17	-1.68
WAH	2006	17	-1.60
WAH	2006	17	-1.58
WAH	2006	17	-1.58
WAH	2006	17	-1.46

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2006	17	-1.39
WAH	2006	17	-1.39
WAH	2006	17	-1.30
WAH	2006	17	-1.29
WAH	2006	17	-1.21
WAH	2006	17	-1.19
WAH	2006	17	-1.17
WAH	2006	17	-1.15
WAH	2006	17	-1.15
WAH	2006	17	-1.13
WAH	2006	17	-0.90
WAH	2006	17	-0.82
WAH	2006	17	-0.78
WAH	2007	18	-2.05
WAH	2007	18	-1.93
WAH	2007	18	-1.88
WAH	2007	18	-1.86
WAH	2007	18	-1.86
WAH	2007	18	-1.68
WAH	2007	18	-1.67
WAH	2007	18	-1.61
WAH	2007	18	-1.59
WAH	2007	18	-1.43
WAH	2007	18	-1.26
WAH	2007	18	-1.26
WAH	2007	18	-1.24
WAH	2007	18	-1.22
WAH	2007	18	-1.21
WAH	2007	18	-1.20
WAH	2007	18	-0.92
WAH	2007	18	-0.85
WAH	2007	18	-0.82
WAH	2007	18	-0.47
WAH	2007	19	-1.63
WAH	2007	19	-1.50
WAH	2007	19	-1.21
WAH	2007	19	-1.10

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2007	19	-1.02
WAH	2007	19	-0.95
WAH	2007	19	-0.89
WAH	2007	19	-0.79
WAH	2007	19	-0.77
WAH	2007	19	-0.77
WAH	2007	19	-0.73
WAH	2007	19	-0.70
WAH	2007	19	-0.68
WAH	2007	19	-0.66
WAH	2007	19	-0.66
WAH	2007	19	-0.60
WAH	2007	19	-0.54
WAH	2007	19	-0.29
WAH	2007	19	0.15
WAH	2007	19	0.43
WAH	2007	20	-1.54
WAH	2007	20	-1.53
WAH	2007	20	-1.49
WAH	2007	20	-1.38
WAH	2007	20	-1.34
WAH	2007	20	-1.32
WAH	2007	20	-1.31
WAH	2007	20	-1.25
WAH	2007	20	-1.24
WAH	2007	20	-1.19
WAH	2007	20	-1.03
WAH	2007	20	-0.90
WAH	2007	20	-0.82
WAH	2007	20	-0.81
WAH	2007	20	-0.67
WAH	2007	20	-0.66
WAH	2007	20	-0.62
WAH	2007	20	-0.39
WAH	2007	20	-0.20
WAH	2007	20	1.68
WAH	2007	21	-1.99
WAH	2007	21	-1.80

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2007	21	-1.60
WAH	2007	21	-1.00
WAH	2007	21	-0.88
WAH	2007	21	-0.63
WAH	2007	21	-0.63
WAH	2007	21	-0.63
WAH	2007	21	-0.48
WAH	2007	21	-0.47
WAH	2007	21	-0.45
WAH	2007	21	-0.45
WAH	2007	21	-0.42
WAH	2007	21	-0.35
WAH	2007	21	-0.30
WAH	2007	21	-0.05
WAH	2007	21	-0.04
WAH	2007	21	0.01
WAH	2007	21	0.35
WAH	2007	21	0.56
WAH	2007	22	-1.02
WAH	2007	22	-0.65
WAH	2007	22	-0.38
WAH	2007	22	-0.30
WAH	2007	22	-0.25
WAH	2007	22	0.12
WAH	2007	22	0.26
WAH	2007	22	0.47
WAH	2007	22	0.63
WAH	2007	22	0.98
WAH	2007	23	-0.83
WAH	2007	23	-0.27
WAH	2007	23	0.03
WAH	2007	23	0.08
WAH	2007	23	0.11
WAH	2007	23	0.29
WAH	2007	23	0.60
WAH	2007	23	0.71
WAH	2007	23	0.96
WAH	2007	23	1.17

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2008	24	-0.36
WAH	2008	24	-0.25
WAH	2008	24	-0.25
WAH	2008	24	-0.06
WAH	2008	24	-0.01
WAH	2008	24	0.02
WAH	2008	24	0.04
WAH	2008	24	0.08
WAH	2008	24	0.17
WAH	2008	24	0.25
WAH	2008	24	0.29
WAH	2008	24	0.34
WAH	2008	24	0.40
WAH	2008	24	0.46
WAH	2008	24	0.46
WAH	2008	24	0.51
WAH	2008	24	0.54
WAH	2008	24	0.58
WAH	2008	24	0.64
WAH	2008	24	0.73
WAH	2008	25	-0.83
WAH	2008	25	-0.78
WAH	2008	25	-0.75
WAH	2008	25	-0.67
WAH	2008	25	-0.66
WAH	2008	25	-0.64
WAH	2008	25	-0.63
WAH	2008	25	-0.61
WAH	2008	25	-0.61
WAH	2008	25	-0.60
WAH	2008	25	-0.52
WAH	2008	25	-0.52
WAH	2008	25	-0.50
WAH	2008	25	-0.50
WAH	2008	25	-0.41
WAH	2008	25	-0.37
WAH	2008	25	-0.36
WAH	2008	25	-0.27

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
WAH	2008	25	0.00
WAH	2008	25	0.52
WAH	2008	26	-1.77
WAH	2008	26	-1.30
WAH	2008	26	-1.05
WAH	2008	26	-0.97
WAH	2008	26	-0.96
WAH	2008	26	-0.96
WAH	2008	26	-0.94
WAH	2008	26	-0.91
WAH	2008	26	-0.89
WAH	2008	26	-0.68
WAH	2008	26	-0.55
WAH	2008	26	-0.51
WAH	2008	26	-0.48
WAH	2008	26	-0.37
WAH	2008	26	-0.32
WAH	2008	26	-0.23
WAH	2008	26	0.02
WAH	2008	26	0.03
CH	2006	27	-2.17
CH	2006	27	-2.16
CH	2006	27	-1.95
CH	2006	27	-1.29
CH	2006	27	-1.17
CH	2006	28	-1.79
CH	2006	28	-1.74
CH	2006	28	-1.60
CH	2006	28	-1.30
CH	2006	28	-0.99
CH	2006	29	-2.33
CH	2006	29	-2.28
CH	2006	29	-2.21
CH	2006	29	-1.70
CH	2006	29	-0.99
CH	2006	30	-0.32
CH	2006	30	0.03
CH	2006	30	0.46

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CH	2006	30	0.53
CH	2006	30	0.73
CH	2006	31	-2.69
CH	2006	31	-1.95
CH	2006	31	-1.94
CH	2006	31	-1.61
CH	2006	31	-1.55
CH	2006	32	-0.81
CH	2006	32	-0.34
CH	2006	32	-0.03
CH	2006	32	0.09
CH	2006	32	0.94
CH	2008	33	-0.79
CH	2008	33	-0.77
CH	2008	33	-0.73
CH	2008	33	-0.59
CH	2008	33	-0.39
CH	2008	33	-0.31
CH	2008	33	-0.16
CH	2008	33	0.05
CH	2008	33	0.19
CH	2008	33	0.20
CH	2008	34	-1.71
CH	2008	34	-1.46
CH	2008	34	-1.03
CH	2008	34	-0.92
CH	2008	34	-0.83
CH	2008	34	-0.77
CH	2008	34	-0.73
CH	2008	34	-0.70
CH	2008	34	-0.47
CH	2008	34	-0.20
CH	2008	35	-0.59
CH	2008	35	-0.41
CH	2008	35	-0.32
CH	2008	35	-0.31
CH	2008	35	-0.09
CH	2008	35	-0.05

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
CH	2008	35	0.19
CH	2008	35	0.23
CH	2008	35	0.28
CH	2008	35	0.33
DH	2007	36	-1.21
DH	2007	36	-1.21
DH	2007	36	-1.09
DH	2007	36	-1.07
DH	2007	36	-1.04
DH	2007	36	-1.04
DH	2007	36	-0.97
DH	2007	36	-0.91
DH	2007	36	-0.89
DH	2007	36	-0.86
DH	2007	36	-0.85
DH	2007	36	-0.79
DH	2007	36	-0.78
DH	2007	36	-0.71
DH	2007	36	0.07
DH	2007	37	-0.95
DH	2007	37	-0.73
DH	2007	37	-0.64
DH	2007	37	-0.63
DH	2007	37	-0.42
DH	2007	37	-0.39
DH	2007	37	-0.34
DH	2007	37	-0.34
DH	2007	37	-0.10
DH	2007	37	0.01
DH	2007	37	0.13
DH	2007	37	0.18
DH	2007	37	0.20
DH	2007	37	0.34
DH	2007	37	0.96
DH	2008	38	0.12
DH	2008	38	0.12
DH	2008	38	0.37
DH	2008	38	0.38

Table E.7. The isotopic ratios of $^{15}N/^{14}N$ (δ) in the residues of plant fiber in feces (n = 578) of caribou in the Central Arctic (CAH), Western Arctic (WAH), Chisana (CH), and Denali herds (DH), late winter, 2006-2008 (pgs. 236-251).

Population	Year	Site no.	$\delta^{15}N$
DH	2008	38	0.49
DH	2008	38	0.54
DH	2008	38	0.57
DH	2008	38	0.69
DH	2008	38	0.69
DH	2008	38	0.71
DH	2008	38	0.80
DH	2008	38	0.90
DH	2008	38	0.93
DH	2008	38	0.98
DH	2008	38	1.07
DH	2008	39	-1.40
DH	2008	39	-1.20
DH	2008	39	-1.12
DH	2008	39	-1.04
DH	2008	39	-1.01
DH	2008	39	-0.90
DH	2008	39	-0.61
DH	2008	39	-0.60
DH	2008	39	-0.58
DH	2008	39	-0.50
DH	2008	39	-0.07
DH	2008	39	0.08
DH	2008	39	0.26
DH	2008	39	0.39